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UNIVERSITY OF ALBERTA

THE DEVELOPMENT OF SOCIAL COGNITION IN FOUR NONHUMAN PRIMATE SPECIES

BY

NANCY E. COLLINGE

A thesis submitted to the Faculty of Graduate Studies and
Research in partial fulfillment of the requirements for the
degree of DOCTOR OF PHILOSOPHY.

DEPARTMENT OF ANTHROPOLOGY

Edmonton, Alberta
Fall, 1991

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Abstract

The present research investigated the development of social cognition in nonhuman primates by applying the model established by Piaget for the study of human infant development. The Piagetian model of development in the sensorimotor or presymbolic period was modified to accommodate nonhuman primate behaviors and to provide a systematic method of investigating the development of naturally-occurring behaviors and skills in social and non-social domains. This method was used in a nine month demonstration case study to investigate the development of a cebus monkey infant living in a captive social group. This study was followed by similar short-term developmental studies of three different primate species, the squirrel monkey, the patas monkey, and the ringtailed lemur. A comparison of the results revealed that, although the acquisition of developmental stages followed the same sequence in all species, there was considerable interspecific variability in the rates of development and expression of social cognition. The variability in the rate and extent of the development could be seen as a function of the following inter-related biological and contextual factors: phylogenetic classification, rate of physical maturation, habitat use, and aspects of the social organization such as the degree of allomothering. The greatest use of social skills were exhibited by the semi-terrestrial patas and ringtailed lemurs whose rapid maturation and early exposure to other females in the group facilitated their development in the social domain.

In many primate species living in large social groups, the development and exercise of social cognition appears to surpass that in the non-social dimension. Possibly the need to understand the many different types of relationships that exist within the group and the demands for appropriate action in social contexts were important factors in the evolution of intelligence in primates.

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Chapter 1. Introduction

The subject of social cognition and the use of social skills in nonhuman primate species has been the focus of a number of recent publications (Strum 1985, Smuts 1985, Byrne and Whiten 1988, Cheney and Seyfarth 1990). Although the extensive social abilities of nonhuman primates are generally acknowledged, there are few research projects providing empirical evidence of social cognition expressed by these intelligent animals.

The standard method for assessing human intelligence for almost a century has been the psychometric approach, which uses various intelligence or mental tests such as the Stanford-Binet test (Kail and Pellegrino 1985). This method has been helpful in determining the educational needs of the individual and also in providing data for the psychometric theory of human intelligence. Although the validity of the early intelligence tests has been greatly improved by the addition of a factor analysis approach to determine the relative importance of different aspects of intelligence, one important limitation of this approach is that it emphasizes individual differences and is insufficient to understand overall intelligence. This approach has also been used in assessing the intelligence of nonhuman primates. For example, there is a long tradition of experiments testing the abilities of monkeys and apes in a variety of tasks dating back to Kluver's (1937) early experiments testing the learning abilities and the sensory acuity of monkeys. Harlow's invention of the Wisconsin General Test Apparatus in the early 1960s introduced an efficient way of presenting discrimination tests providing proof that monkeys learn to learn, in that they form strategies to solve similar problems (Haraway 1989). These experiments, which test "performance knowledge" (Thomas and Walden 1985:187), have demonstrated learning and reasoning abilities, visual discrimination, memory, and many other mental capabilities in the nonhuman primate subjects.

The information processing approach to the study of human intelligence is the more recent method used by many psychologists in the field. Information processing theory attempts to define the manner in which knowledge is organized and accessed, and differs from the psychometric approach in that it emphasizes the manner in which mental tests are accomplished rather than the level of achievement (Kail and Pellegrino 1985). Kluver and many other psychologists designed their intelligence tests for nonhuman primates with the specific objective of determining the mechanisms by which the tasks were being accomplished; in effect looking at the way the information was being processed (d'Amato and Salmon 1984, Rumbaugh and Pate 1984).

The use of the Wisconsin General Test Apparatus and other methods of testing nonhuman primate intelligence are particularly unsuited to the investigation of social cognition since they are carried out on individuals in a non-social setting. This arrangement is also true for those experiments set up to investigate the manner in which the individual animals process the knowledge required to perform their tasks.

The present research project has attempted to circumvent the difficulties inherent in testing the use of social cognition in primate species by applying the developmental approach to the study of human intelligence. The advantages of this method are that it can be carried out on infants in a social setting, and is designed to investigate the social dimension in the development of intelligence.

The first comprehensive theory of intellectual development was articulated by Jean Piaget in the early part of this century, and modifications of his cognitive-developmental model are still in use today (Kail and Pellegrino 1985). "The Piagetian model sheds light on the problem of a general theory of intelligence, defines stages and levels of intellectual activity across a variety of domains" (Parker and Poti 1990:220). The ever-increasing number of psychologists and primatologists using this model to investigate nonhuman primate cognitive development is a clear indication of its applicability as a valid methodological tool. The strength of the Piagetian approach is that it provides a systematic way of recording infant development which can be used effectively with human and nonhuman primates.

It is interesting to note that this type of research, using a theory of human intellectual development as a standard by which to test and compare animal intelligence, is a reversal of the typical research design in comparative psychology. The usual research protocol involves the investigation of a behavior or an ability in an animal subject such as a rat or a pigeon, in order to shed some light on the human condition.

The present study has been designed to provide some insights into the use of social cognition in nonhuman primates by investigating the development of social skills in conjunction with the development of motor and practical skills, making use of the Piagetian cognitive-developmental model in the research design. The rationale for the use of this human-oriented model will be fully discussed in Chapter 2. In addition, Chapter 2 lays the philosophical foundation for the project which will hopefully clarify the need to address the subject of social cognition in primate species.

Chapter 3 describes the methodology used in the longitudinal study of infant development in four nonhuman primate species in the present project. This chapter includes a description of the manner in which the Piagetian model was applied, and the way in which the critical behaviors characterizing the attainment of each developmental stage were chosen. Chapter 4 describes the use of the Piagetian model in the investigation of the development of an infant cebus monkey; and focuses on the development of social cognition, using the results of the demonstration case study. Chapter 5 deals with the analysis and discussion of three shorter-term developmental studies on infants of different primate species, testing the usefulness of the Piagetian model in comparisons of developmental patterns between species particularly in the social dimension. The final chapter relates the implications of the present research findings and the research of others in the field of social cognition to the theoretical discussion of the evolution of primate intelligence presented in Chapter 2.

Chapter 2. The Study of Social Cognition: Theoretical Considerations

Themes in the Evolution of Primate Intelligence

In the opinion of a number of primatologists, psychologists, and philosophers, one of the main functions, if not the main function of intelligence is that it facilitates group living in highly social animals such as nonhuman primates (Jolly 1966, Humphrey 1976, Kummer 1982, Mason 1982, Box and Fragaszy 1986). Primates are noted for their large brains, particularly in the neo-cortical area, compared to mammals of similar size (Jerison 1973). Given that the brain is an extremely energy-expensive organ to operate, there must have been a major adaptive advantage for the expanded neo-cortical functions found in primates (Gibson 1986); however, everyone does not agree with those who propose that this major adaptive advantage occurred in the social domain. There are two main theories regarding the evolution of the flexible, creative intelligence generally attributed to members of the Order Primates, the "social origin" theory and the "ecological origin" theory. Some researchers argue that ecological pressures, such as foraging and feeding strategies or the successful avoidance of predators, selected for higher intelligence (e.g. Clutton-Brock and Harvey 1980, Gibson 1986, Milton 1988), while others suggest that the social pressures associated with group living provided the major impetus for the evolution of cognitive abilities (e.g. Jolly 1966, Humphrey 1976, Burton 1984, Jolly 1988). Intelligence is a multifaceted ability (Whiten and Byrne 1988), likely to defy any theory that rests on only one factor in explaining its evolution, and a case could be made for both the ecological or social scenario. Clearly, ecological and social factors had an input into the evolution of primate intelligence; and the relative contribution of these agencies would almost certainly vary with the species, depending on their adaptive strategies. This chapter will present a discussion of both the "ecological origin" and the "social origin" theories; however, because the present study is directed towards the development of social cognition, the latter theory will be more fully explored.

Ecological Origin Theory

Milton (1988) reviews the evidence from a number of field studies to add validity to her argument that successful foraging behaviors provided the impetus for the evolution of primate intelligence. She uses the following facts about food availability in the tropical forest to develop her hypothesis:

a. Diet is related to home range size. Since leaves are not as patchily distributed as ripe fruit, folivores generally require a smaller foraging area than frugivorous species.

b. Potential plant food items are patchily distributed in space, with the great diversity of tree species being distributed in clumps rather than in a uniform fashion.

c. Potential plant food items are patchily distributed over time, the availability of high quality food such as ripe fruit being typically short-lived.

d. The problems associated with the patchiness of the food supply in time and space are somewhat lessened by the fact that the patchiness can be predicted.

The last fact may have acted as an important factor in the development of a complex brain, since the ability to predict the availability of plant food in the tropical forest likely requires a greater mental capacity than that required by secondary consumers like carnivores in their quest for food. There would be selective pressure to promote efficiency in the search for food, such as strategies for foraging that combine the lowest expenditure of energy and time with the least risk of exposure to predators. The need to respond to changing environmental conditions and to form contingency plans would be included in the pressures selecting for behavioral flexibility requiring enhanced cognitive abilities.

To demonstrate the implications of this theory (that species dependent on diverse, sparsely available foods should show greater mental capabilities than those relying on uniformly available resources) Milton (1988) refers to field studies of howling monkeys and spider monkeys living sympatrically on Barro Colorado Island. The basic needs of the two species differed, with the howlers eating fruit in season but reverting to folivory when fruit was scarce, and the spider monkeys depending on a diet of fruit regardless of the availability. The location of preferred foods presents a greater problem for the spider monkeys, and requires the use of a more complex foraging strategy. Milton herself (1988:288) notes the important role a cohesive social group plays in the transmission of the necessary ecological information, and she suggests that the howlers are able to learn the preferred foods and how to obtain them from their mothers and others through imitation and observation. Spider monkeys, on the other hand, travel in small foraging parties; and are dependent on their mothers for a much longer period. They learn their foraging skills primarily from their mothers, although the location of high quality food sources also comes from the members of the foraging party. Milton's (1988) contention is that the spider monkeys appear to have a much richer repertoire of social behaviors and gestures due to their individual needs to receive and convey information about food species and locations.

The advocates of the ecological point of view often refer to correlations between relative brain size and diet (Milton 1988, Clutton-Brock and Harvey 1980), stating that folivorous species, which presumably do not need sophisticated foraging strategies, generally have smaller brains relative to body size than frugivorous species. Milton (1988) notes that since there is very little association between brain size and sociability, and that it is difficult to see why there would be the clear relationship that exists between brain size and diet if social factors were responsible for expanded intelligence. Although it is argued that folivorous and frugivorous species likely have similar social pressures, the latter aspect of their life-ways has not been adequately investigated.

By virtue of their superior foraging skills and manipulative capabilities, cebus monkeys provide further evidence in support of the ecologically-oriented theory. Parker and Gibson (1977) suggested that adult cebus monkeys demonstrate an ability for complex object manipulation that is not context-related and can be generalized to a number of situations. From the available data it appears that this ability far exceeds that shown by any other nonhuman primate species excepting chimpanzees. Using a model established by Jean Piaget for the investigation of sensorimotor intelligence in human infants, Parker and Gibson (1977:623) described the manipulative abilities of cebus monkeys as "tertiary sensorimotor intelligence" which was defined as truly intelligent object manipulation. Cebus are able to recognize possible sources of embedded food; and use a number of tactics requiring cortically-mediated coordinations to find, extract, and process the food (Gibson 1986). Gibson (1986) suggests that these monkeys exhibit planning abilities in their foraging techniques; for example, they appear to damage some fruits in order to speed the ripening process. It has been shown that there is a correlation between brain size (particularly the neo-cortex) relative to body size and "omnivorous extractive foraging habits" (Gibson 1986:97), as demonstrated by primate encephalization and neo-cortical indices recorded by Stephan (1972). The encephalization and neocortical progression indices refer to the extent that size of the brain and the neo-cortex exceed that predicted for insectivores of similar size (Stephan 1972). In both of these measures cebus monkeys are on a par with chimpanzees, ranking second only to humans (Gibson 1986).

The use of innovative foraging strategies and complex object manipulations does not appear to be related to omnivory alone. It is well documented that omnivorous cebus and squirrel monkeys spend a major portion of their daily activity budget moving around the tropical forest foraging and feeding; however, their foraging patterns are very different. Cebus monkeys are noted for their abilities to find and extract food items from inaccessible places, while the more restless squirrel monkeys rely on speed and agility in their quest for food.(Parker and Gibson 1977, Izawa 1980, Terborgh 1983). Macaques and baboons, which are also highly omnivorous species, do not appear to show the same degree of complexity in their manipulation of objects in natural situations (Parker and Gibson 1977). Parker and Gibson (1977) believe that tertiary sensorimotor intelligence would be selected for in situations where the availability of high quality nutritious food was constrained by seasonal variations and inaccessability . They suggest that "once intelligence evolved, it would allow broad application of complex object manipulation schemata" (Parker and Gibson 1977:637) which presumably includes the manipulation of social and physical objects.

Social Origin Theory

Sawaguchi and Kudo (1990) examined the relationship between the relative size of the neocortex (RSN) and social structure in a number of prosimian and anthropoid species. They found significant positive correlations between group size and RSN in prosimians. When they controlled for diet in their anthropoid subjects, among frugivorous species, those living in polygamous groups showed a significantly larger RSN than monogamous animals. These findings prompted them to infer a close association between social structure and the degree of neocortical development, with the accompanying implication that complex social groupings could have selected for greater neocortical development, particularly in the prefrontal area. This relationship between RSN and social structure is particularly striking in hominoid species, with the monogamous gibbons exhibiting a far lesser degree of neocortical development than the polygamous chimpanzees (Sawaguchi and Kudo 1990).

Wynn (1988) reviewed one of the traditional hypotheses for the evolution of human intelligence, that the selective pressure came from tool use and the need for increasingly more sophisticated technology. The basis of this hypothesis is the premise that, in the genus Homo, the development of technology approximately paralleled the development of the brain. However, Wynn (1988) suggests that the evidence for the evolution of the brain from endocasts and the archeological evidence are not sufficient to provide a clear correlation between the increasing size of the brain and improvements in technology. He points out that most of our technological achievements - from compound tools to computers, from animal husbandry to irrigation agriculture - came well after 300,000 years ago "when the evidence we have argues against any marked increase in intelligence" (Wynn 1988:282). The fact that some of the most taxing problems confronting humankind today are of a socio-political nature, leads Wynn (1988:284) to argue that "it seems just as reasonable to suppose that this kind of behavior selected for intelligence, as it is to suppose tools selected for intelligence".

An increasing number of scholars from different disciplines have promoted the notion that social pressures were a potent force in the evolution of primate intelligence (Whiten and Byrne 1988). In nonhuman primates, some of the most convincing evidence lies in the use of social knowledge to mediate interactions and to cement relationships. As previously stated, primates are social animals living in a variety of social groups, ranging from small to large and complex; and this variability can exist within, as well as between, species (Mason 1976, Poirier 1977). Mason (1982) feels that the important issue is not what sort of social grouping a species usually exhibits but how social groups maintain their social order, cohesiveness, and continuity in the face of changing physical and social conditions. Primate social relationships are more complex because, compared to animals of similar size, primates live longer, are dependent on their mothers or caretakers for longer periods, and have developed the capacity for individual recognition during the long socialization process. Field research generally indicates that this is so, especially in studies of species such as chimpanzees and Japanese macaques, where particular groups have been the subjects of long range studies. Cheney and Seyfarth (1990) have demonstrated in experiments with wild vervets that these monkeys can not only recognize individuals (a capacity common to most invertebrates), but can also recognize relationships between other members of the social group. Using a hidden tape recorder to play back the screams of a two-year old juvenile, they were able to determine by the mother's response that she recognized the screams of her offspring. Other adult females in the area responded to the screams by looking at the mother, indicating that they were able to associate the vocalizations with a particular juvenile and recognize the relationship between the female and her infant. This result suggested to Cheney et al. (1986:1363) that the vervets not only "could distinguish their own offspring from others but could recognize the associations that exist among other group members".

Kin recognition, which is defined in terms of preferential treatment towards known relatives, is a generally accepted faculty of a number of taxa, from insects to rodents to primates (Gouzoules 1984). Gouzoules (1984) explored the following four possible mechanisms that have been put forth to explain how animals and insects might recognize related conspecifics; (1)spatial distribution, (2) association during development, (3) phenotype matching, and (4) recognition of alleles. She noted that, although many of the theoretical approaches to kin recognition have focussed on the last two innate operations (phenotype matching and allele recognition), the most convincing evidence from animal research has indicated that familiarity during development is of prime importance in kin discrimination. There is ample evidence of kin recognition in many insect, reptile, and animal species; however, the recognition of kin relations of others seems to be discussed only with respect to primates (Gouzoules 1984). The field experiments of Cheney and Seyfarth (1990) on vervet monkeys discussed above, and similar playback experiments conducted by Gouzoules et al.(1986) on rhesus macaques, show that, at least in these species, the animals are aware of social relationships which include the kin relations of others. Dasser's (1985) laboratory research indicated that socially-experienced female *Macaca fascicularis* could not only recognize mother-infant pairs from their social group, but could classify members of the same matriline from 35 mm. slides.

Recent field work by Smuts (1985) and Strum (1987) clearly indicates that savannah baboons use sophisticated social strategies for their own benefit. Anestrous adult female baboons will maintain lasting "friendships" with one or more adult males, providing added protection and care for themselves and their offspring (Smuts 1985). Strum (1987) reports that male baboons require extensive social skills to maintain their place in a given social group or to gain a place in another troop.

From laboratory experiments it appears obvious that nonhuman primates have mental capacities beyond those used in the wild; and as Humphrey (1976) points out, we do not usually find superfluous capacities in plants and animals. Therefore we must look for a biological function for intellect, and this function might be socially-oriented.

Living in a social group, for all its advantages, presents many problems that must be solved using some form of intellect for calculating the consequences of one's behavior in a social interaction (Humphrey 1976).

Humphrey (1976) argues that animals living in complex social groups require creative intelligence to hold their societies together. Maintaining social life is one of the most urgent aspects in the organization of an individual's behavioral repertoire, and an individual must be able to assess others in the group and make proper adjustments based on the behaviors of the others in the interaction (Humphrey 1976). Most complex activities in a primate's life are social, because in order to live successfully, an individual must learn to cope with the behaviors of "others" (Altmann 1965). Monitoring social situations and making the appropriate adjustments to insure the successful outcome requires cognitive abilities. Many have suggested that skill in managing social situations was critical in the evolution of cognition (Jolly 1966, Humphrey 1976, Seyfarth 1982), and that "social life preceded and determined the nature of primate intelligence" (Jolly 1966:506). Perhaps the minds of social animals were selected to provide for self-knowledge or introspection leading to a knowledge of others based on an analogy to their own behavior. Since the ability to deal with others may sometimes mean a life or death decision for the individual, it would seem logical to assume that there would be strong selection for such an ability (Humphrey 1976).

Primates must have knowledge about the behavioral tendencies of their conspecifics in the achievement of certain goals, and often use members of their group as "social tools" (Kummer 1982). This "social tool use" requires more flexibility and finesse than mechanical tool use because in the former, the tool has goals of its own and these can change during the interaction between the user and the tool (Kummer 1982).

An analysis of social interactions between classes of animals has given some indication of the diverse abilities required by individuals in a social group. Kummer and Goodall (1985) cite examples of cognitive tests on pigtail macaques which indicate that low-ranking animals learn more efficiently and faster than high-ranking animals. They suggest that subordinate group members have made greater use of their genetic potential for learning because of their greater need for alliances and subterfuge to gain access to mates and resources. This type of research indicates the likelihood of variability in the degree to which cognitive abilities are used by different group members. Kummer (Kummer and Goodall 1985) suggests that, since the ultimate result of selective pressures is a mentally flexible primate, it would be useful to look at the situations in which this ability is most effective.

Dominance in primates is often discussed in terms of social rather then physical attributes such as size and strength. There are a number of reports in the primate literature of old, ill, or physically weak individuals who are in a position of dominance in their social group (Fedigan 1982). Fedigan (1982:102) argues that, although a strong healthy body would be an advantage, "the power of social learning and social tradition is so pervasive in primates that it often overrides the importance of physical factors in the determination of dominance rank".

A position of dominance often confers an advantage to the individual in terms of access to resources such as space, mates, or food, although dominance in terms of access to one resource does not necessarily confer an advantage in all areas (Fedigan 1982). Janson (1985) reports that, in *Cebus apella,* whose creative intelligence is so evident in their foraging strategies, dominance rank can be related to fitness. The feeding bouts of dominant animals are uninterrupted by aggressive encounters with conspecifics, and their central position in the group affords them more

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protection from predators. In dominant females, the greater access to food appears to contribute to an enhanced ability to raise more of their infants to four years of age (two of three infants) compared to subordinate females (one of four infants) (Janson 1985:135).

Older, high -ranking individuals not only appear to have social skills which allow them to influence others in the social group, but they often have knowledge of sources of water or food that could be accessed in times of drought. Hauser (1988) documented such a case in vervets, where a technique presumably to soften tough acacia pods was first observed in an old dominant female during a severe long-term drought in Amboseli National Park in Kenya. The technique, which involved soaking the pods in an exudate found in tree crevices, spread throughout the adult females and juveniles in the troop and was used extensively only during the period of water shortage.

Jolly sums up the the ecological/social origin controversy nicely when she reflects on her original article, "Lemur social behaviour and primate evolution", published in 1966 in the light of new findings about lemurs:

> "Since the early study, lemur society has proved to be far more complex than I guessed in 1965..........Meanwhile lemurs continue to seem uninterested in technology....Thus if one accepts the 1965 argument that lemur's social skills reflect the original primate bias towards social intelligence, then the studies of the intervening years reinforce that point of view" (Jolly 1988:75).

Proponents of the "social origin" theory argue convincingly that ecological pressures, even the need for inventive techniques for obtaining embedded food, could be managed by "practical" intelligence (Humphrey 1976); and "practical problems that face higher primates can, as in the case of termiting, be dealt with by learned strategies without recourse to creative intelligence" (Humphrey 1976:306). Humphrey's main thesis is that the large fund of practical knowledge required by primates can be readily acquired in a social context which favors the transmission of knowledge.

The question of the relative contribution of social or ecological agencies to the evolution of primate intelligence will likely remain unanswered. It is really a "Which came first, the chicken or the egg?" type of question, where we cannot say with confidence that either pressure provided the selective impetus. What can be said however, is that intelligence in extant primates allows for a behavioral flexibility that can be applied to both social and non-social domains.

Definitions

A cognitive view of animal behavior sees animals as information processors, capable of adapting to the physical and social environments using their cognitive skills (Roitblat 1985). "These skills include learning, remembering, problem solving, rule and concept formation, perception, recognition and others" (Roitblat 1985:2). Several experimental studies of nonhuman primate behavior have used cognitive concepts arising from human mental experiences such as semanticism, mental maps, and deception; and attempt to use these concepts to explain or at least theorize about the intelligent qualities of animal behavior (Menzel 1971, Premack and Woodruff 1978, Whiten and Byrne 1988).

Before discussing the concepts useful in a study that specifically addresses animal cognition, it is important to establish some guidelines for the use of the terms. Neisser's (1967) definition of cognition seems to be suitable for the purposes of the present study. He described cognitive processes as those by which sensory input is transformed, reduced, elaborated, stored, recovered, and used. Cognition therefore refers to the acquisition and the use of knowledge. Since a number of dictionaries define intellect in terms of the use of knowledge (see Oxford Illustrated Dictionary 1962:421), and since much of the literature related to animal mentation uses the terms cognition and intelligence interchangeably, this will be the practice in the present study.

The Study of Social Cognition in Nonhuman Primates

There is ample evidence for the impressive mental capacities of nonhuman primates. Comparative psychologists who have tested the intellectual capabilities of many animal species in a number of laboratory tests have shown that nonhuman primates are generally adept in several areas such as problem-solving, discrimination learning, transitivity, concept formation, and spatial memory; and have indicated the use of symbolism , displacement, deceit and even self-recognition in some species (Essock-Vitale and Seyfarth 1987). Because it is clear from the evidence of field and laboratory studies that nonhuman primates are capable of sophisticated social strategies in the wild and can master many tasks in the laboratory, it is not surprising that there has been general agreement concerning the need for an investigation of the use of intelligence in social situations. The field of social cognition is recognized as an important area for study in human psychological investigations, as it should be in the field of animal behavioral studies.

Since Humphrey's 1976 article, which advocated the investigation of correlations between social complexity and individual intelligence, Mason (1979, 1982), Fragaszy (1985), Essock-Vitale and Seyfarth (1987), and most recently, Byrne and Whiten (1988), are among the primatologists who have strongly indicated a need for research on social intelligence in primates.

Clearly, although the need was recognized decades ago, very little has been done to fill this gap. The problem, which is also generally recognized, is that a methodology which satisfactorily combines the need for empirical evidence and the ability to describe multifaceted social interactions has not been found. Goodall (1985), Strum (1985), and many others have provided a wealth of evidence describing the use of sophisticated social strategies in chimpanzees and baboons. The problem, however, is that the evidence *is* only descriptive; and subject to the criticisms of those who seek more rigorous scientific proof (Kummer 1990). Essock-Vitale and Seyfarth (1987:452) cite three problems facing researchers embarking on such a study, "we would need (1) a means of recognizing intelligent behavior and distinguishing it from other activities; (2) an objective way to measure intelligence, and compare it across different behaviors and species; and (3) an objective way to measure the complexity of social interactions."

Mason (1982:140) states that at present "we lack a detailed and comprehensive understanding of the development and exercise of 'social intelligence' for even one species". Since the difficulties associated with the quantitative study of the "exercise" of social intelligence seem insurmountable, perhaps an investigation of the development of social behaviors in conjunction with the development of intellectual capacities and other skills would provide a viable alternative. The social development of the infants within their physical limitations and the constraints of the social and physical environments in which they are raised, is an important area for research (Mason 1979). This is especially true in the case of nonhuman primates, where it has been suggested that the relatively long period of socialization and the importance of social learning makes it relevant to consider the relationship between the development of social behavior and cognitive abilities (Box and Fragaszy 1986, Parker 1977).

Kummer et al.(1990:87) describe two kinds of social cognition: "Knowledge of the social structure of the animal's own group, and knowledge about mental states of other group members". During the early developmental period, when the infant is spending most of its time with its mother, it will begin to gain some knowledge of the network of social relationships within the group by observing the mother's interactions with kin and unrelated animals. A study of the development of the infant's interactions with others should provide some insights into the onset of social cognition and the contextual factors affecting it.

Such a study must pinpoint the appearance of social behaviors, and distinguish between reflexive behaviors and those that require insight and intention. Strum (1985) and others have carefully documented the development of social skills in specific categories of animals, such as juvenile male baboons; but the actual day by day, week by week development of social intelligence from infancy has never been systematically recorded and analyzed. Plooij's (1982) comprehensive study of the development of free-ranging chimpanzee infants focused on a comparison of the behavioral ontogeny with that of human infants and not on social development per se.

In order to initiate such a study, a systematic method of investigating infant development is required, one which will allow the research to be replicated and the results compared. The problems cited by Essock-Vitale and Seyfarth (1987) would be much easier to circumvent with the developmental approach, because the complete behavioral repertoire of the infants can be documented from birth. The changes in behaviors over time from simple, non-volitional behaviors to more complex, goal-directed activities in social and non-social domains should be more easily detected and measured.

A Cognitive-Developmental Model Applied to Nonhuman Primates

Following Harlow's early research with rhesus monkeys (Harlow et al.1963), the social development of a number of species of nonhuman primate species has been investigated with particular emphasis on the importance of the mother in the socialization of the young. However, a comparison of the results across species is difficult because of the different methodologies and environmental conditions (Hinde 1971). A model involving the observation of behavior that has proven useful in the study of human development was pioneered by Jean Piaget, a Swiss psychologist who studied the intellectual development of his own and other children; and observed that it proceeded by stages which were characterized by certain predictable abilities and deficits (Parker 1977). He divided human intellectual development into the following four periods from birth to adolescence:

(1) The Sensorimotor Period, which extends from birth to approximately 2 years of age, during which the perception of and interactions with the environment shape the child's view of the world;

(2) The Pre-Operational or Pre-Conceptual Period, covering the period from two to seven years of age. In this period, reason is dominated by perceptions, and the child uses intuitive rather than logical solutions to problems;

(3) The Concrete Operational Period, which occurs from ages seven to eleven years, at which point thinking is bound to real rather than abstract operations. The child can now understand mathematical transformations and the concept of conservation of liquids; and the

(4) The Formal Operational Period, which covers the period from 11 to 15 years of age. The adolescent is now able to deal with hypothetical cases and deductive reasoning, and is capable of complete generality of thought (Piaget and Inhelder 1969, Lefrancois 1989)).

The period that interests primatologists is the sensorimotor or presymbolic period, during which the intelligence of the young individual is shaped by early interactions with the environment. Piaget's stages, specifically in the sensorimotor period which deals with action-oriented activities, have been used in the investigation of motor and cognitive development of some nonhuman primate species on the assumption that there are striking parallels in human and nonhuman primate infant development (Chevalier-Skolnikoff 1976, Parker 1977). He described the growth and development of human infants in the sensorimotor period in six separate series or domains: the sensorimotor intelligence; the object-concept; the spatial; the temporal; the causal, and the imitation series (Piaget 1952). During the presymbolic period each of these series is made up of six qualitatively different behavioral stages , which develop sequentially and appear concurrently; for example, the appearance of the third stage of the spatial series coordinates with the appearance of the third stage of the object-concept series (Piaget 1952). The basic premise of his model is that, although the age of acquisition of the stages varies across infants, the sequences are invariant.

The application of Piaget's stages to the development of humans and animals has been criticized by many, mainly because of the difficulties of imposing discrete stages on a continuous developmental process (Brainerd 1978, Essock-Vitale 1987). Brainerd (1978) suggested that Piaget's use of stages is acceptable as a description of behavior, but falls short as an explanatory vehicle because of the problems involved in measuring causal as well as behavioral changes. He argued that the resulting claims are circular in reasoning; e.g., an infant is said to be in Stage 2 of the object-concept series because he or she is capable of Stage 2 behaviors. However, others feel that the application of consistent cognitive principles to the behaviors of each particular stage avoids the problem of circularity (Kinsbourne 1978, Chevalier-Skolnikoff 1977).

Parker (1977) defended the use of Piagetian stages to describe the timing and appearance of behaviors, and to compare the development of species-specific abilities. She stated that "Whereas other conceptual frameworks offer insight into some aspects of behavioral organization, Piaget's model offers insight into virtually all aspects of behavioral organization" (Parker 1977:43-44). It is particularly powerful because it is a structural theory that focuses on the organizational level of behavior, the organizations being constructed during development from simple inherited patterns (Parker 1977, Wynn 1989). Parker (1977) adapted the stages of sensorimotor development to fit nonhuman primate behavioral patterns, particularly those related to unstereotyped behavior and intelligence. This approach provided a developmental model that could be used for cross-species comparisons of manual, locomotor, and cognitive schemes, their coordination and application (Parker and Gibson 1979). Chavalier-Skolnikoff (1976, 1977) has used the Piagetian model in the investigation of the origins and evolution of language, and as a tool to describe and compare the socialization process in humans, monkeys, and apes. She feels that this model of human intellectual development during the sensorimotor period "provides a systematic and objective framework for comparative studies" (1977:159), which encompasses simple to complex behaviors independent of age, and combines the description of behaviors with a functional approach to behavioral analysis.

Antinucci (1989b:10) felt that "the general principles governing cognitive organization Piaget developed and substantiated along this long work represent the ideal tool to pursue the study of cognition". This model was used exclusively in the investigation of the cognitive development of three nonhuman primate species in his recently edited publication, _Cognitive Structure and Development in Nonhuman Primates_ (1989a).

Scarr (1983) suggests that there is generalized patterning and timing in the development of intelligence in human and nonhuman primate infants, and that these show a high degree of similarity especially in the presymbolic (sensorimotor) period; any variation is due to species-specific patterns, individual variability, and environmental conditions. However, later in life, adults show vast differences in adaptations which seem to indicate qualitatively different cognitive abilities. Both human and nonhuman primate infants are extremely curious and open to learning compared to other mammals, and set about learning in a "graded sequence of intellectual stages" (Scarr 1983:195); but, although the pattern of development in the sensorimotor series of human infants is similar in closely-related primate species, there are differences in the degree of maturity at birth, the flexibility of learning, and the length of the socialization period. The restrictions on the flexibility of learning depend on genetic preadaptation and developmental adaptation; and although environmental inputs are necessary, basically the direction of development is hard to deflect, and the individual will develop only within the limits of its inherited potential (Scarr 1983).

Piaget's model is useful in describing developmental stages in nonhuman primates because it takes advantage of an ethological method of observing overt behaviors of the infant in its social setting, and uses these behaviors as parameters of the level of behavioral organization operating in the individual (Parker 1977). Etienne (1973), who used Piaget's stages to investigate object-permanence in animals other than primates, also agrees that this model of cognitive development can be useful in the study of animal behavior. He particularly approves of Piaget's notion that, at any age, a young individual's cognitive processes reflect a total organization of structure allowing only certain behaviors to occur. Cognitive development is not only determined by the maturation of the nervous system but depends on a continuous interaction between the individual and the environment. This development can be divided into sequential stages, the organization of one leading to and integrated into the next stage (Etienne 1973). The ages at which these stages occur are unimportant because there are a number of environmental factors which act on the individual. The important fact is that the stages follow each other; and although the time-frames may be different, individuals from different backgrounds will move through the same general sequence (Etienne 1973).

In the Piagetian model of development some of the early behavior patterns remain, some regress, and others are repeatedly applied to different situations. Piaget refers to features of the behavioral patterns that appear consistently as schemes, which are the units of the infant's behavioral repertoire. The development of behavior is based on the differentiation, generalization, and the coordination of the infant's first reflex-like schemes (Piaget 1952). Each stage can be recognized by the emergence of new schemes, which in many cases are variations of the old ones (Parker 1977). Etienne (1973) feels that the idea of 'schemes' is useful because it refers to a particular unit of an individual's behavioral repertoire at any specific developmental level, and argues that the value of Piaget's model lies in the "value of its predictions and its heuristic impact" (1973:373).

Piaget's early training was in the field of biology, and he based his developmental theory on the biological principle of adaptation by means of assimilation and accommodation (Piaget 1952, Thomas and Walden 1985). These concepts are used by Piaget (1952, 1955) to explain the developmental process. Whereas an organism adapts to the environment by constructing new forms, intelligence is developed by building mental structures which can deal with environmental agencies

(Piaget 1952). Stimuli are understood in terms of pre-existing knowledge, and are absorbed or assimilated into an existing behavioral structure, which is in turn adjusted or accommodated to the stimuli, resulting in a change in the system (Piaget 1952). In other words, the organism incorporates the stimuli from the environment into its existing structures and readjusts them, allowing it to adapt to the external world (Hart and Mason 1973). Development is necessarily conservative because the young individual can only assimilate stimuli into an existing behavioral repertoire (Parker 1977, Mason 1979).

Piaget's (1952) definition of the stages of development combined the following two concepts:

1. The hierarchy of development, in that the stages succeed each other in a fixed order and
2. The equilibrium towards which an organism tends to develop, and which can only take place within the limits of the behavioral structure for each stage.

This need to achieve equilibrium dominates the coordination of the internal structures which will allow the infant to understand external events. Therefore, the outside world is perceived in terms of the infant's ability to assimilate information from it, rather than as it actually is (Case 1985). The result is a transition from one state of temporary equilibrium to a succeeding one due to the continuing effect of assimilation and accommodation (Hart and Mason 1973). "Intelligence is only a generic term to indicate superior forms of equilibrium of cognitive structuring" (Piaget 1952:6-7). The increased ability of the individual to behave flexibly in response to environmental agencies is an indication of the increasing differentiation of structures by the integration of new structures into existing ones. The achievements of one developmental stage are consolidated in preparation for new behavioral patterns, each stage representing a completed level of organization (Hart and Thomas 1973).

The neonate can detect sights and sounds; and react to pain, tastes, and smells, with little concept of the world around it and little memory store; but it possesses sensory systems and cognitive propensities that render it a self-reinforcing, information-processing organism (Lefrancois 1989). The infant represents a system that seeks out and responds to stimulation and by so doing builds up a repertoire of behaviors and capabilities (Lefrancois 1989).Piaget (1952) argued that knowledge does not come from the object or the subject but from the interactions between them;.therefore knowledge is tied to actions. The changes in behaviors arise from the integration of the genetic input (sensory systems and cortical maturation), environmental factors, and continuous self-regulation. At the end of the sensorimotor period, when the infant is approximately two years old, Piaget (1952) considers it to be intelligent as far as the coordination of actions is concerned.

In summary, the Piagetian cognitive-developmental model appears to be well suited to an investigation of the development of social cognition in nonhuman primates for the following reasons:

1. It is systematic in that the basic ideas form a coherent, integrated system (Case 1985).

2. It is parsimonious, in the sense that it uses few constructs in explaining development (Case 1985).

3. It is not reductionist and does not ignore the differences between higher and lower intellectual function (Case 1985).

4. It is an extremely testable model because it makes specific predictions about the developmental process in children. These predictions have been tested and retested by developmental psychologists who generally have confirmed his findings, particularly the order of the stages in the sensorimotor period (Lefrancois 1989). Lefrancois (1989:220) states that " there is impressive agreement

concerning the major acquisitions and the sequences in which they appear in Piaget's sensorimotor period".

5. The basic principles are still in use in human social cognition studies (Chandler 1982, Harter 1982).

6. It has been used successfully in studies of nonhuman primate infant development (Parker 1977, Antinucci 1989b).

Leading child psychologists, I.C. Uzgiris and J.M. Hunt, were particularly interested in the effect of rearing conditions on cognitive development. They investigated a method of assessing the cognitive development of infants that would avoid the use of standard Development Quotient (D.Q.) tests to predict I.Q. because these tended to ignore environmental aspects during development and "assume a predetermined rate of development" (Uzgiris and Hunt 1975:15). Since Piaget's work illustrated how easily-observed behaviors could be used to indicate the presence of a cognitive structure and how changes in the reaction to a given situation could imply a change in the cognitive grasp of the situation, they used his concept of sequential developmental stages as a starting point.

Uzgiris and Hunt (1975) feel that the evidence of a number of child psychologists supports the idea that a definite sequential order exists in psychological development which is invariate across individuals. They developed an ordinal scaling method of assessing infant development "based on the appearance of critical behaviors which were designated as landmarks of implied levels of achievement and organization along several branches of development" (Uzgiris and Hunt 1975:14). Their classification system of six ordinal scales, replacing Piaget's series of development in the presymbolic period, encompassed a greater range of elicited behaviors than were available under a Piagetian system, many of which are explicitly designed for children and would not be applicable to nonhuman primate infants (Spinozzi and Natale 1989). However, their idea of establishing critical behaviors which would characterize levels of achievement in the different series or domains, would seem to provide a useful way of applying the Piagetian model to a developmental study. The concurrence of Piaget's stages of development in the various areas did not concern Uzgiris and Hunt because they were interested in predicting the effects of rearing conditions and environmental factors in certain areas of development. It can be argued that such a investigative technique would be useful to predict variability in patterns of development due to species differences or differences in physical and social environments.

The present study applies the Piagetian cognitive-developmental model to the description of the development of social cognition in conjunction with other skills in infant nonhuman primates by defining critical behaviors which signal the acquisition of the stage of development in social and non-social domains. These specific behaviors which are described in Chapter 3 were adapted to fit the physical and cognitive abilities defined by Piaget (1952) for each of the series in Stages 1 through 6. The critical behaviors are general enough to be applicable to infants of any nonhuman primate species, thus allowing for interspecific comparisons of developmental milestones.

The Relationship of Brain Structure to Intelligence

Gibson (1977) has coordinated a theory of cortical development with Piaget's model of human intellectual development in the sensorimotor period. Intelligence, according to Parker and Gibson (1977), is the end product of the development of behavioral programs which allow an individual to invent a new procedure, or use an old one in a new context to solve problems. Basic neurological capacities form a necessary foundation for the acquisition of the behavioral parameters described by Parker (1977) in her modification of Piaget's stages of development. The cerebral cortex is necessary for mediating intelligent activity; but intelligence also depends on the combined function of all parts of the brain, including cortical and sub-cortical areas (Gibson 1977). Gibson (1977) suggests that the basic components of intelligence gained in the sensorimotor period are the ability to differentiate motor actions and perceptual data, the ability to handle simultaneous and sequential motor actions and perceptual data, flexibility in reactions to stimuli, and the ability to internalize motor and perceptual data and to anticipate and compare the results of actions based on the internalized perceptions. She argues that research has shown that cortical areas mature in a sequence which parallels the development of these parameters of intelligence, beginning with motor and primary sensory areas, continuing with the premotor and sensory association areas, and ending with the frontal, temporal, and parietal association areas. This section deals with Gibson's hypothesis concerning the coordination of brain and behavioral maturation; and unless otherwise stated, the reference used is Gibson (1977) "Brain Structure and Intelligence".

In the newborn, the motor actions and sensory perceptions are undifferentiated and involuntary, and lacking in sequential or simultaneous coordination. Myelination, or "the process by which a nerve fibre acquires a myelin (lipoprotein) sheath which surrounds the nerve fibre and increases the efficiency of the fibre function" (p.128), is used as one measure of neural maturation; and it appears that the cortex is relatively unmyelinated at this point. The motor cortex, which controls the ability to perform fractional movements and determines the force and speed of the muscle contraction, is the most advanced cortical area in the neonate, but the undifferentiated quality of the infant's actions indicates that it is still quite immature.

Gibson hypothesizes that the increasing differentiation of the motor function and behavior in the young individual can be explained by looking at the sequence of maturation of the different cortical layers. The neurons of the cortical areas are arranged in layers I to VI from the surface inward, with all cortical areas except the motor cortex having six layers. It has been shown that in rhesus macaques and human infants, the sequence of maturation is VI, V, I, IV, III and II; however, in the monkey, layers V and VI of the motor cortex are partially myelinated at birth. The pattern of maturation indicates that the output layers (V and VI) mature first, followed by the input layers (II-IV). Motor cells and fibres mature slightly before sensory cells and fibres in monkeys and humans, a fact which lends support to Piaget's (1951) theory that early motor actions provide the perceptual data for the infant.

Given that maturation or myelination begins in the lower layers of each cortical area and spreads outward gradually, with all areas functioning at some level once any one area becomes mature, it should be possible to relate behavioral and cortical development. Thus, Gibson suggests that, like Piaget's stages of behavioral development, each cerebral layer interacts with the succeeding layers and becomes modified. The observable result is not a linear succession of behavior patterns with one behavior ceasing and another one beginning, but the appearance of new behavior patterns which are added to old ones, altering them or combining with them.

There are a number of similarities in the stages of sensorimotor development in the human and monkey infant, but one of the most obvious differences is the much more rapid maturation of the infant monkey. A result of this relatively rapid maturation is a more evident overlap in the stages of development in the infant monkey, since a rapidly developing cortex leaves less time to lapse between the maturation of the different areas. Another important difference in human and nonhuman primate ontogeny is the obvious speed with which infant monkeys develop their locomotor skills. The sequence of maturation of the cortical areas is similar in macaques and humans, in that the motor cortex develops earlier.

However, locomotion is not controlled by the cortex alone, and since the cerebellum and the basal ganglia play an important role, it is possible that the sub-cortical areas also mature more rapidly in the macaque.

Gibson argues that that there is clearly a basic difference in the form of intelligence displayed by nonhuman primates and humans during development and adulthood. The increased size of the cerebral cortex, particularly the parietal, temporal and frontal association areas in the human brain, would seem to provide a greater overall intelligence. In the human brain there is also a decrease in neuronal density and an increase in dendritic branching. Although the relationship between this neurological reorganization and the behavioral differences between human and nonhuman primates has never been established, one possible implication of the increased capacity for neuronal interactions in the human brain is an enhanced ability to process information. The greater branching of the motor neurons in the human spinal chord could result in a greater differentiation of activities, while the significantly larger human parietal and temporal association areas possibly allow for an expanded capacity in humans to perceive and anticipate sequential relationships. The frontal lobe, which mediates behaviors characterizing intellectual capacity, is also much larger in humans, allowing for more behavioral flexibility and a greater ability to internalize and anticipate the future.

Parker (1977) and Antinucci (1989b) noted that the main deficiency in the development of sensorimotor intelligence in nonhuman primates compared to that of human infants was the complete lack of repetitive (circular) actions with respect to objects and object-object coordinations. The primary or rudimentary circular reactions, which according to Piaget deal with repeated actions involving single body parts such as the hands, feet, and mouth, are much the same in young monkeys and human infants (Parker 1977, Antinucci 1989a). Young monkeys, however, never seem to show any tendency to shake a rattle repeatedly, swing a toy, turn a spigot or the like for pleasure or in play as a child would. Piaget (1952) suggests that human infants display repetitive actions with objects to maintain an interesting effect which they have discovered by accident. It is also possible that these actions could be encouraged by parents or caretakers (Vauclair 1981). Vauclair (1981) argues that the social environment provides reinforcement to human infants as to the appropriate object manipulation, something that has never been observed in nonhuman primates. In the developmental study carried out by Parker (1977), it was clear that the infant monkey's repetitive actions usually involved physical activity, suggesting a kinesthetic reinforcement. Objects were bitten, chewed, or climbed on repeatedly by the young monkeys and apes, but rarely played with in the human sense. In the later stages of development many of the monkey's trial and error behavior patterns were related to locomotor or social activities (Parker 1977).

It was clear from Parker's study that the young monkey practised new locomotor activities as it was developing, while less active human infants focus on developing skills with object manipulation. The monkey's lack of repetitive actions related to objects could be merely due to the fact that these actions are not stimulating, rather than to a cerebral deficit. It could be argued that the proprioreceptive stimulation gained from the excessive physical activity observed in young monkeys would surpass that derived from manipulating an inert object. Gibson suggests that a neurological explanation for the difference in the capacities for primary, secondary, and tertiary circular reactions may be that the cortical areas controlling them may function differently in monkeys,apes and humans. Clearly the parallels in the correlation between the development of the cerebral cortex and behavioral development, which Gibson suggests can be identified in human and nonhuman primates, is only valid in the infantile or, using Piagetian terminology, the sensorimotor period.

The "Decalage" Debate

In Piaget's model, one of the basic assumptions is that the level of understanding in a number of domains requires the application of the same logical operations, and therefore the stages in the respective series appear relatively simultaneously (Piaget 1952, Case 1985). Later research in child development indicated the presence of horizontal decalage, or time-lags, in the acquisition of cognitive stages across domains (Jackson et al.1978, Case 1985). This discovery prompted psychologists to investigate the whole question of decalage in general, and in particular the special case of disparity between the acquisition of object permanence and person permanence. (Jackson et al.1978). It was hypothesized that, since people could be seen to provide the developing infant with a higher level of stimulation in their affectionate and frequent interactions, person permanence would develop more rapidly than object permanence (Jackson et al.1978, Dore and Dumas 1987). However, a number of psychologists working with children and infants have shown that these results were biased, due to factors or variables such as task differences and past experience, which had been largely ignored. Research by Jackson et al.(1978) indicated that the decalage in the development of object and person permanence is very dependent on practice, task differences, and task content; and when these are taken into account, there is no disparity in the acquisition in social and non-social domains. They admit that when decalage does appear, person permanence precedes object permanence, but that this is not a stable tendency.

The major impact of this research was to emphasize the importance of environmental and contextual factors in the stages of cognitive development (Jackson et al.1978).

Therefore, with children, perhaps a general correlation in the acquisition of the stages of development could be expected. However, if the results indicate the presence of a decalage, then the effects of contextual factors should be investigated (Jackson et al.1978). The investigation of any decalage in the stages of development across domains in infant nonhuman primates could provide useful information regarding the effects of environment and rearing conditions on the cognitive development in social and non-social areas.

The Theoretical Background to the Study of Social Cognition

Piaget viewed cognitive and social development as parallel processes, with behaviors directed towards people and objects reaching similar stages at approximately the same time (Piaget 1962, Serafica 1982). The infant is said to acquire a de-centered perception of the environment in the social and non-social domains, and becomes able to perceive objects and events or individuals in relation to itself in any number of possible states and locations (Dasser 1985). Although Piaget recognized the importance of social interaction in an infant's sensorimotor development, he did not place any special emphasis on the development of social knowledge (Chandler 1982); and much of the early research into human infant development was centered on the assessment of competence in interactions with physical and non-social objects (Dore and Dumas 1987, Smith 1988).

Until 1960 there were few attempts to differentiate between social and general knowledge; however, in the mid 1960s, developmental psychologists became interested in the relationship between social and cognitive development, and "social cognition" was recognized as a new and vital field of research in child psychology (Serafica 1982, Smith 1988). The early studies in social cognition were directed towards investigating the trends and sequences in the social-inferential abilities of children, focusing on how children perceive others (Serafica 1982). The results indicated a relationship between social-inferential abilities and logical thinking, but psychologists were hard-pressed to prove the existence of parallels between social-inferential abilities and social behavior because the possible areas of study were so diverse. This situation created difficulties in measuring social behavior.

By the mid-1970s, the emphasis in social cognition research shifted towards understanding the relationship between cognitive and social functioning (Serafica 1982). A number of psychologists were convinced that social knowledge was very different from non-social knowledge, involving different procedures and structures (Chandler 1982). Social cognition was viewed as more than just the use of cognitive skills in a social situation, and it was argued that special skills were needed to act appropriately with others (Dasser 1985). This view was challenged by cognitive-developmental theorists who adhered to the Piagetian tradition, and who maintained that cognition is 'content-free' and can be applied in social or non-social domains (Chandler 1982:224). Since empirical proof of the nature of cognitive structures, social or non-social, has not been established, the question of the character of knowledge in the two domains has never been clarified, and indeed is no longer the central issue. Recent research has been aimed at confirming the presence of social cognition and the development of the use of social intelligence in a number of different situations; e.g., understanding social rules, interpreting the intentions of others, moral behavior, etc. (Chandler 1982, Harter 1982, Shantz 1982).

Similar questions have been raised in developmental research in nonhuman primates, and Dasser (1985) suggests that the abilities of nonhuman primates to respond appropriately to complex social situations and to distinguish between different categories of individuals and their relationships to each other corresponds closely with abilities used in the non-social domain. She feels that the superior learning abilities and excellent memories shown by primates in laboratory tests would be sufficient to allow the animals to perceive, remember, and compare the amount of information for social competence, whereas humans possibly use a more specialized type of cognition related to social knowledge gained by introspection. It is not at all clear that nonhuman primates are self-aware and capable of introspection, or have the capacity for decentration described by Piaget (Dasser 1985). However, Cheney and Seyfarth (1985, 1990) strongly defend the premise that social necessities selected for higher intelligence and that there is a special type of intelligence reserved for use in social situations. To emphasize their point they cite the amount of training needed for nonhuman primates to acquire competence in laboratory learning tests, as opposed to the relative ease with which they are able to master similar abilities in their behaviors with conspecifics.

The distinction between the social and non-social domains could be merely rhetorical. If these types of cognition reflect different systems, it is clear that, in many instances, there is a functional relationship, in much the same way that CNS and endocrine systems are separate but function together through the hypothalamic-pituitary connection (Rutter 1985). Therefore the important issue would seem to be, that if the distinction is crucial to the research question, then the social and non-social variables must be clearly separated (Rutter 1985).

Although a number of psychologists interested in social cognition challenge aspects of Piaget's theories of human child development, it is clear that his cognitive developmental model is still being used as an investigative tool (Harter 1982, Chandler 1982, Selman et al.1982, see Turiel 1983:62 for a review of the research). It has been suggested that, if this framework is to be used effectively, the role of the environment and contextual factors in social and cognitive development must not be overlooked (Serafica 1982, Turiel 1983). Turiel (1983) states that, in order to define social development adequately, it is particularly critical to understand the culture in which a child is being raised. The fact that nonhuman primate societies are not overlaid with the same type of cultural rules as human societies should make the effects of environmental and contextual factors on infant development much clearer. Even in the 1980s, the cognitive-developmental model pioneered by Piaget was an accepted investigative tool for developmental research which could be applied to the nonhuman primate case.

Chapter 3. The Adaptation of the Piagetian Model and Delineation of Critical Behaviors

The objectives of this project were twofold:

1. To use the case study approach to investigate the development of social cognition in an infant non-human primate.

2. To use this investigation as a demonstration project or model, set up specifically for the purpose of establishing a systematic and standardized method of assessing the development of nonhuman primate infants in both social and non-social domains. This scheme was designed in such a way as to be applicable to behavioral studies of infant development of any nonhuman primate species. Thus it should be possible to determine interspecific variability in infant development, and also to demonstrate the effects of environmental and contextual factors on the developing infants of a particular species.

The scheme established in the demonstration project was then tested on other species, by conducting additional short term studies, and also by using the pertinent information from the developmental studies of other researchers.

The original case study was conducted on a captive infant cebus monkey being raised by its mother in an ongoing social group. Cebus monkeys are a particularly useful species for a study of this type for a number of reasons. The cognitive abilities of adult cebus have been thoroughly tested in the laboratory; and it has been demonstrated that they show object permanence, can visually discriminate objects with different shapes and colors, can generalize to other objects, master delayed matching-to-sample tests indicating a good short-term memory, solve problems associated with opening puzzle boxes, and many other capabilities (Davis 1974, D'Amato and Salmon 1984, Simons and Holtkotter 1986). Parker and Gibson (1977) suggested that adult cebus monkeys are able to attain Stages 5 and 6 of

Piaget's sensorimotor intelligence series, which allows them to perform complex object and social object manipulations and discover ways to extract food items by active exploration. Westergaard and Fragaszy (1985) have shown that capuchins will spontaneously begin to use objects introduced into their enclosure as tools. Parker and Gibson (1977, 1979) argue that cebus monkeys can be ranked with the higher apes in their ability to use tools intelligently, and relate this ability to an adaptation for omnivory and feeding on highly seasonal and embedded foods. The fact that cebus monkeys live in complex, multi-male multi-female social groups would indicate that their cognitive abilities are useful in a social sense as well as in food procurement; e.g., for recognition of their own kin and the kin relationships of others, remembering the results of past interactions, and knowing their place in the dominance hierarchy (Jolly 1979).

It was noted in Chapter 2 that there is a correlation between brain size (particularly the neo-cortex) relative to body size and omnivorous extractive foraging strategies (Gibson 1986); and according to the primate encephalization and neocortical progression indices reported by Stephan (1972) cebus monkeys are on a par with chimpanzees, ranking second only to humans. Parker (1977) indicated that she regards cebus monkeys as superior to Old World monkeys in their intellectual capacity, a judgement which would suggest that they would be ideal subjects for a demonstration project addressing the development of sensorimotor, object-concept and social intelligence. In fact, infant *Cebus apella* have been the subjects of recent studies of early object-concept development using the Piagetian model (Spinozzi 1989, Schino et al.1990).

A zoo environment should provide an excellent opportunity to investigate social development, given the fact that the animals are assured a constant food supply and are able to spend more time in social interactions than members of a wild group (Bernstein 1971). It is possible that their cognitive abilities would prove particularly useful in accommodating to life in a confined area. The study of a zoo colony permits a degree of accurate quantification and control not possible in the field, while preserving a somewhat natural grouping under less impoverished conditions than those often found in experimentally controlled laboratory studies (Hinde 1971).

A Modification of the Piagetian Model to Accomodate Nonhuman Primate Development

Parker (1977) investigated the development of an infant stumptail macaque using Piaget's model for assessing human infant development and adapted it to accommodate non-human primate behaviors. Since an infant macaque displays behavior patterns which are very different from those of a human infant, Parker had to decide if Piaget's six series of development in the sensorimotor or pre-symbolic period were applicable to monkeys. Piaget considered the successive stages in the different series inter-related, and included a number of the same behaviors in more than one series because they could apply to different aspects of behavioral organization. Parker (1977) concluded that, since many of the same behaviors were found in the object-concept, spatial, and temporal series, three series (the sensorimotor-intelligence, the object-concept and the imitation) would be sufficient to record the development of an infant monkey and make adequate comparisons with human development.

These series can be described as follows:

1. Sensorimotor-intelligence refers to practical intelligence, and this series follows the development of the ability to deal with perceptions derived from sensory input in an increasingly efficient manner. Sensorimotor activities are action-oriented, and this series describes the development of the infant's understanding of the world in terms of its perception of the world and interactions with it (Lefrancois 1989).

2. The object-concept series, which deals with object permanence, is particularly important in infant cognitive development because it is the one area that is fundamental to the child's concept of the world (Lefrancois 1989). Object permanence refers to the ability to perceive that an object has substance and constant dimensions; and that, although it may appear different under different conditions, it is the same object (Piaget 1954, Antinucci 1989c). The ability to

perceive the constancy of objects is closely tied to the concept of space, since objects have a spatial component in their relationship to the individual.

3. The imitation series (Parker 1977) refers to actions executed by the infant after watching them performed by another animal. Clearly the pattern must be present in the infant's behavioral repertoire before it can carry out a successful imitation.

The following five series were chosen to describe the development of the nonhuman primates in the present study; the sensorimotor-intelligence, the object-concept, ther spatial, the locomotor, and the social series. The causal series was omitted from the present investigation, as it was from Parker's (1977:63) on the grounds that it was "too interpretive". Since the primary focus of the this study was the development of social cognition based on the observation of naturally-occurring behaviors, I found it necessary to include a social series, which replaced the imitation series, as well as a spatial and a locomotor series. The imitation series provided important insights into the cognitive development of the infant; however, since imitation necessarily takes place in a social context, it was incorporated into the social series.

It was important to use the spatial and locomotor series, along with the sensorimotor-intelligence and object-concept series, in order to describe the activity patterns of young nonhuman primates satisfactorally. The behavior patterns defined for the social series were chosen to provide a description of the development of interactions with members of the social group. The spatial series included behavior patterns that indicated the the infant's increasing knowledge of the physical environment. At first the infant was spatially-oriented to its mother's body; but it soon became aware of the non-maternal world, and spatial cognition became increasingly important. This series marked the transition from the perception of space as practical and egocentric space to space containing bars, walls, trees, branches, and cagemates as well as the subject itself. The locomotor series described the emergence and use of the necessary motor skills. Clearly, the spatial series and locomotor series are closely related, especially in the later stages of development, since complex locomotor skills require an extensive knowledge of space. However, it was important to separate the two series in the early months of life before the appearance of independent locomotion when the infant was gaining its first knowledge of its environment.

Parker (1977) and Chevalier-Skolnikoff (1976), who compared the development of monkeys, apes, and humans, found that the transition from one stage to another could be precisely defined by noting the appearance of certain "critical" behaviors. Such behaviors would possess all of the characteristics of a particular stage of development. During each stage, the frequency of the new behavior patterns increases from zero to a relatively high level; then in some cases declines when the features of the next stage begin to appear (Chevalier-Skolnikoff 1976).

Piaget (1952) used the terms primary, secondary, and tertiary to describe motor acts that pertain to the body, objects in the environment, and object-object interactions respectively; and added the adjective 'circular' to refer to motor acts that were repeated. Although young non-human primates often show primary circular reactions (repeat self-oriented motor actions), they rarely act repeatedly with an object in the environment (show secondary circular reactions), as do human infants (Parker 1977, Spinozzi and Natale 1989). They repeat motor actions, presumably for the kinesthetic pleasure derived, but rarely bounce a ball or shake a rattle over and over again like small children. Tertiary circular reactions, which are defined as repeatedly using one object in relation to another object or a field of force like gravity, do not seem to be part of a young monkey's usual repertoire. Parker (1977), however, retained the term because some of the monkey's actions, such as banging an object on the ground, are characteristic of this type of behavior pattern. She modified the descriptive terms to fit monkey behaviors by adding the adjective 'linear' to describe non-repetitive actions which involve the serial use of one or more behavior patterns. For example, Parker (1977) would describe the use of a number of actions such as rubbing, turning, and chewing observed in the manipulation of an object as a 'derived secondary linear reaction'.

Since infant non-human primates show more complex physical actions than human infants, Parker (1977) used the term 'body schemata' to describe voluntary locomotor patterns, such as leaping from one surface to another, which are never seen in human infants. 'Meta-behavioral parameters' (Parker 1977:84) are the organizational aspects of behavior that combine to make up a behavioral pattern; and basic to the developmental model is the concept that each stage can be recognized by the manifestation of these parameters in new and different ways. The metabehavioral parameters that Parker described for each stage are as follows; type of coordination, locus of the coordination, the number of acts included, the volition of behavior, goal determination, temporal and spatial patterning, context of behavior pattern, origin of stimulus, and releasing and reinforcement of stimulus. Subsequent to Parker's (1977) developmental study of an infant stumptail macaque using the Piagetian model, a number of other researchers have used the stage concept to describe the development of other non-human primate species (Chevalier-Skolnikoff 1977, Poti 1989, Spinozzi 1989, Spinozzi and Natale 1989; see Natale and Antinucci 1989:98-99 for a review of other investigations of object-concept development).

The major difference between the present study and those of Piaget and others who have applied his model, was the exclusive use of data which were based on observations of naturally-occurring behaviors without any contact with the subjects, rather than the reactions of the infant to a situation elicited by the researcher. Although the previous studies included observations of spontaneous behaviors, some of the research was conducted with the investigator interacting on a one-to one basis with the infant, having set up a situation which would demonstrate its behavioral abilities or deficits. Although this technique has proven successful in describing cognitive development, it does not provide information regarding the development of behaviors in the social domain. The exclusive use of naturally-occurring behaviors not only allows for the investigation of development in a social group, but greatly increases the applicability of the model to the studies of both wild and captive animals.

Clearly, the use of this investigative technique would be best adapted to field studies in which the birth dates of the infants are known and where the animals are relatively visible. These studies would include research on species which have been studied continuously such as Japanese macaques, rhesus macaques, and chimpanzees; and also African species living in open country such as baboons, vervets, and patas monkeys.

Since the investigation of behavior is the only way to assess the capabilities of an animal, it is important to use a model allowing us to describe the animal's approach to everyday situations (Candland and Keys 1986). In the case of the infant primate, human or non-human, Piaget's model appears to have merit, provided the behavioral data are collected consistently over the sensorimotor developmental period. The appearance, durations, frequencies, and sequences of specific behaviors, charted week by week, should provide a record of motor, cognitive, and social development which can be described in stages and used for inter- and intraspecific comparisons.

Criteria for the Selection of Critical Behaviors Defining Each Developmental Stage

The viability of using a Piagetian model for the study of infant development in non-human primates depends on the choice of valid, readily observable behavior patterns to define the attainment of the stages of development in each of the different series or domains. The description of these critical behaviors in the present study combines the criteria used by Piaget (1952) for the achievement of each stage by human infants, and the "metabehavioral parameters" outlined by Parker (1977:83)) which, she suggested, can be used to define the level of achievement in each Piagetian stage in both human and non-human primate infants. She defined the following metabehavioral parameters as " aspects of behavioral organization which remain implicit in behavioral descriptions" (1977:83).

Because the present study was designed to record naturally-occurring behaviors only, many of the behavioral units used to define the appearance of each stage are necessarily different from those described by Piaget, Parker and others in experimental situations. The choice of critical behaviors used in the present study was based on the application of the following metabehavioral parameters which were defined by Parker, and the following list is an abbreviated description of those set out by her (Parker 1977:81-83):

1. Type of Coordination - the nature of the interaction between parts of the self alone; the self and social or physical objects.
2. Locus of Coordination and Applications - the parts of the body acting and the parts of the social object or physical object/substrate acted upon.
3. Volition of Motor Patterns - the degree of choice exerted between different alternatives.
4. Differentiation of Motor Patterns - the degree of separation of the various components of a behavior pattern.

5. Number of Acts in a Behavior Pattern - the number of actions easily identified in the motor coordination.

6. Goal Determination - the degree of choice exerted between alternative goals.

7. Contexts of Behavior Pattern Application - familiarity or novelty of the setting in which the behavioral schemes occur.

8. Temporal/Spatial Patterning of Behaviors - the position, orientation, sequence, frequency and repetition of the acts.

9. Releasing and/or Reinforcing Aspects of Stimuli or Actions - the response or feedback from the subject's own actions resulting in a repetition of the response to the stimuli.

10. Source of Stimuli Eliciting the Behavior Patterns - the source of the stimuli associated with the beginning, repeating or continuation of an action.

It is important to note that, using the Piagetian model of the stages of development, many of the behavior patterns observed at the various stages do not cease. Some remain in the infant's behavioral repertoire, becoming increasingly more efficient, while others are incorporated into more complex behavior patterns. Thus, there is no abrupt end-point to any one stage; only the beginning of behaviors which meet the metabehavioral parameters of the next stage (Chevalier-Skolnikoff 1977, Parker 1977).

The following section describes the stages of development and provides a definition of the criteria used to establish the critical behaviors in Table 3.1 (See Appendix 1 for a complete description of the behavioral units). It will be noted that, in some instances, the same critical behaviors are used in two different series. As Piaget (1952) indicated, some series are closely inter-related, and the same behavior may apply to an aspect of behavior in different areas. This situation is particularly evident in the sensorimotor-intelligence and the object-concept series since the development of the notion of object permanence is so vital in the use of sensory input involved in interactions with the

Table 3.1. Critical Behaviors for Developmental Stages

Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Stage 6
Sensorimotor-intelligence Series					
Nipple Contact Ventral Cling Move on Mother Random Movements Suck Thumb Undir. Scratch Undir.	Suck Thumb Directed. Scratch Directed. Look Around Loose V.Cling Feel Environ. Feel Body Part	Clutch Environment. Rub Surface Eat Solid Food Pick up & Release. Play Face-Non-social Pick up Food	Rub & Eat Simple Process. Close Visual Examination.	Complex Food Process Visual Search	Problem Solving-Activity
Object-Concept Series					
Nipple Contact Ventral Cling Suck Thumb Undir. Scratch Undir. No Observable-Reaction to Objects	Feel Environment Lick Surface Chew Surface Chew Body Part Feel Body Part	Clutch Environment. Solitary Play Rub Surface Pick up & Release. Pick up Food Drop and Pick Up	Rub and Eat Simple Process. Tactile Search Manipulation Self-Groom Close Visual Examination	Displ.Experiments Complex Food Process Visual Search Play with Medium Insert Item-Retrieve Item Hand in Aperture Hand/Hand Transfer	Problem Solving-Activity
Spatial Series					
Nipple Contact Ventral Cling Move on Mother Change Position	Loose V.Cling Look Around Feel Environ. Lap Sit Mother Sit Beside Mo.** Away from Mo >1m.**	Dorsal Cling Stand Locomote Climb Away from Mo.<1m.**	Complex Climb Locomotor Play Jump Reverse Field	Locomotor Games Plan Locomotion Insert Item-Retrieve Item	Direct Choice of Route to Circumvent Barriers
Locomotor Series					
Move on Mother Change Position	Crawl on Environ. Crawl on Other Circle Mother	Hang Locomote Climb Hop	Complex climb Locomotor carry Locomotor play Jump	Locomoter Games Plan Locomotion	Direct Choice of Locomotor Action to Acheive Desired Result
Social Series					
Grmed by Others Muz. by Others Nip.Contact Mo. Vent. Cling Mo. Move on Mother	Feel Cagemate Lap Other Chew Other Lick Other	Nip.Contact Others. Crawl on Other V.Cling Other Muzzle Social Play Mother. Dorsal Cling Other. Play Face(Social) Social Clutch Dir.Aggression Grab Object from Other Threat Imitate	Groom Mother Groom Other Vis.Exam Other Loc. Play(Soc) R.& T.Play Follow Initiate Play Seek Nip.Other Fear Grimace	Display Mount Fight Pres. for Groom	Direct Choice of Social Action to Acheive Desired Result

** Measures of proximity to mother, not behavioral units environment. This inter-relationship can also be seen in the spatial and locomotor series, since an infant must develop spatial knowledge before it can successfully operate in the environment.

The metabehavioral parameters described for each developmental stage are summaries of those defined by Parker (1977:96-101).

Stage 1

Sensorimotor Intelligence Series

Reflex Actions, Intercoordinations, and Adaptations to the Maternal Environment (Piaget 1952, Parker 1977) These behaviors consist of reflex actions in terms of the infant's own body; e.g., waving feet and hands in the air, opening and closing the mouth, moving the tongue in and out. The intercoordinations and adaptations to the environment at this point are confined to behaviors like suckling, random scratching movements, clinging to the mother, and rooting on her body. At this point, the infant does not have any notion of "self", and therefore all of its activities are centered on its own body and bodily needs (Piaget and Inhelder 1969).

Object-Concept Series - The Absence of Behaviors to Vanished Objects (Piaget 1955, Parker 1977))

No observable reaction to any environmental object.

Spatial and Locomotor Series -

No spatial concept outside of the individual's own body and that of its mother. The infant's motor actions are restricted to movements on the mother's body.

Social Series - The Emergence of Self-Directed Behaviors (Cowan 1978).

The infant is a social object for the animals who muzzle, groom and stare at it; however, these actions elicit no reaction from the infant.

Metabehavioral Parameters for Stage 1

1. Type of Coordination - reflex
2. Locus of Coordination - mother and self

3. Volition of Motor Pattern - none; actions are involuntary
4. Differentiation of Motor Pattern - undifferentiated, global
5. Number of Acts- single acts in a behavior pattern
6. Goal Determination - no goal
7. Context of Behavior - mother's body
8. Temporal/Spatial Patterning - oriented to mother's body, no particular sequences of behaviors, repetition without control.
9. Releasing and/or Reinforcing Aspects - consumatory stimulation.
10. Source of Stimuli - Internal state of the infant.

Critical Behaviors for Stage 1

Sensorimotor-Intelligence Series- Suckle, Ventral Cling, Head Fall Back, Tongue Protrusion, Open and Close Mouth, Wave Arms and Legs, Suck Thumb Undirected, Scratch Undirected, Flex Hands and Feet.

Object-Concept Series- No observable reaction to any environmental object.

Spatial Series- Undirected Look Around, Move on Mother, Change Position.

Locomotor Series- Move on Mother, Root, Change Position.

Social Series- Suckle and Ventral Cling (Mother); no reaction to the social advances of others, e.g., muzzling and grooming.

Stage 2

Sensorimotor-intelligence Series - Primary Circular Reactions and Rudimentary Adaptations and Intercoordinations to the Environment (Piaget 1952, Parker 1977).

The reflex processes are progressively integrated into cortical activity and the behavior patterns observed in Stage 1 are now coming under voluntary control (Piaget 1952); e.g., the infant no longer roots around on the mother's body but can move directly to the nipple, and thumb sucking is no longer due to a chance encounter between the thumb and the mouth. The infant displays a number of primary circular reactions (repeated actions directed towards the infant's body), and interacts more frequently and efficiently with the environment. It begins to finger the substrate in an undirected fashion but can aim its scratching movements.

Object-Concept Series - The Absence of Behaviors to Vanished Objects (Parker 1977)

The infant begins to look around a great deal, but does not appear to seek any particular visual image. It does not look around if an object disappears from view and is only able to follow slowly moving objects. The infant does not appear to notice if a physical object or another animal has moved from its line of vision, and its behaviors could be described as "out of sight, out of mind".

Spatial and Locomotor Series

New behavior patterns are directed towards the mother and the environment, as the infant begins to crawl around the substrate and the mother's body.

Social Series - Primitive Voluntary Adaptations to Social Objects

Undirected social actions appear at this stage as the infant reaches out to touch other animals, but at this point there seems to be no perception of itself as an entity separate from other physical or social objects (Cowan 1978). The mother is still the center of its social universe; and, although it moves onto the substrate, it rarely loses contact with her.

Metabehavioral Parameters of Stage 2

1. Type of Coordination - some voluntary control of reflexes, some rudimentary contact with the physical and social environments, visual following of moving objects.
2. Locus of Coordination - self to self, self to mother, self to substrate and environmental objects.
3. Volition of Motor Patterns- primitive voluntary.

4. Differentiation of Motor Pattern - undifferentiated.

5. Number of Acts - the behavior pattern consists of two acts

6. Goal Determination - none

7. Context of Behavior Pattern - familiar, mother oriented.

8. Temporal/Spatial Patterning - repetition of some basic motor patterns, main orientation is still towards mother, no observable sequence of actions, some undirected actions towards the environment.

9. Releasing and/or Reinforcing Aspects - pleasure in feedback from kinesthetic and proprioreceptive stimuli.

10. Source of Stimuli - feedback from visual and tactile stimuli.

Critical Behaviors for Stage 2

Sensorimotor-intelligence Series- Suck Thumb Directed, Scratch Directed, Look Around, Loose Ventral Cling, Feel Body Part, Feel Environment

Object-Concept Series- Feel Environment, Feel Body Part, Lick Environment, Chew Environment.

Spatial Series- Loose Ventral Cling, Look Around, Feel Environment, Lap Sit (Mother), *Sit Beside, *Away from Mother > 1 m.

Locomotor Series- Crawl on Environment, Circle Mother.

Social Series- Feel Other, Chew Other, Lick Other.

*Measures of proximity to mother, not behavioral units.

Stage 3 -

Sensorimotor-Intelligence Series - "Secondary Linear Schemata" (Parker 1977:71),"Procedures Destined to Make Interesting Sights Last" (Piaget 1952:153) and The Coordination of Vision and Prehension (Parker 1977).

The infant now begins to rediscover interesting effects originally found by chance, a development which marks the beginning of intentional behavior. Piaget (1952:148) defined intention as it related to Stages 3 to 5 behaviors that are "determined by conscious desire or by the direction of the act, the awareness being itself a function of intermediary acts necessitated by the principle act".In the monkey, this effort to "rediscover" often takes the form of repeating motor actions rather than repeatedly acting on an environmental object; e.g., the accidental discovery of the interesting effects of hanging upside down and swinging from a bar as the result of a near fall. This early idea, of an action related to an effect, has been termed "magical phenomenalist" (Piaget and Inhelder 1969:18), because as yet the infant has no real notion of causality. The fact that two events happen sequentially is sufficient to make them appear to be related.

One of the major accomplishments of this stage is the development of hand-eye coordination allowing the infant to show more accommodation to moving objects, and to pick things up and clutch at branches and other animals more efficiently. At this stage, the infant can be seen picking up small objects and reaching for bits of food, involuntarily dropping an object and voluntarily picking it up.

Object-Concept Series - The "Beginning of Object-Permanence and Extending the Movements of Accommodation" (Piaget 1954:13)

The beginning of the idea of the permanence of objects "marks progress in the solidification of the universe depending on action" (Piaget 1954;13). At this point, the concept of object permanence is linked to the actions that the infant is perpetrating on the object. The infant can watch a rapidly moving object, showing an understanding of the existence of the object; but this development is just an extension of the infant's accommodation to that object. If there is no action directed to an object, it is not perceived to exist permanently. The infant is now able to pick things up and clutch at the bars or branches more efficiently; and will reach for a dropped object and bring it into its line of vision. It begins visual and manual examinations of parts of the environment including other animals, and begins to spend time interacting with them.

Spatial Series - The infant begins to ride upright on the mother's back, which gives it a greatly expanded view of the world and a better orientation in space. The improved coordination between prehension and vision and improved depth perception allow the infant to become more familiar with its space and the objects in it. As the infant becomes more confident of its hand-eye coordination, it greatly extends its use of space and expands the number of motor patterns used.

Locomotor Series - A number of new motor patterns which are not analogous to human infant behavior appear here, as the young monkey becomes more familiar with its world and begins to climb, hop, walk, and run quadrupedally.

Social Series - The Beginning of Intentional Independence of Actions in a Social Situation (Cowan 1978)

This is the first truly social stage, as the infant is now able to direct its attention to animals (Cowan 1978) when they approach; and it begins to muzzle, chew, and otherwise interact with nearby conspecifics. The young monkey actively searches for social behaviors which prolong social interactions and produce an interesting effect. Social facilitation begins at this stage, as the infant begins to watch other animals closely and attempt to incorporate their actions into its own behavioral repertoire. At this point, other animals are used in a practical sense, as a large part of the infant's social activities are directed towards reaching out and snatching food from others. New facial expressions, such as the play face, also appear at this stage

Metabehavioral Parameters of Stage 3

1. Type of Coordination - reciprocal or simultaneous coordination of two acts with each other, and coordination of actions in two sensory modes e.g. visual and tactile.

2. Locus of Coordination - controlled actions from self to environmental objects (social or physical) or substrate.

3. Volition of Motor Patterns - control of simple acts, voluntary choice.

4. Differentiation of Motor Patterns. -rudimentary differentiation, breakdown of global patterns.

5. Number of Acts - two or three actions in the behavior pattern.

6. Goal Determination - fortuitous goal.

7. Context of Behavior Pattern - familiar, but with added incentive to repeat behavior.

8. Temporal/Spatial Patterning - some recognizable simple sequences of behaviors, with repetition of these patterns to perpetuate the effect. Actions are directed to an increasing number of environmental objects and areas.

9. Releasing and/or Reinforcing Aspects - contingency reinforcement; feedback is from the pleasure gained from new activity patterns.

10. Sources of Stimuli - self-induced stimuli, as well as stimuli from the social and physical environments.

Critical Behaviors for Stage 3

(A number of the same behaviors are found in both the sensorimotor-intelligence and the object-concept series because in Stage 3 the beginning of the idea of object permanence is linked to the motor actions directed towards objects).

Sensorimotor-intelligence Series- Clutch Environment, Rub Surface, Eat Solid Food, Pick Up Dropped Object, Pick Up and Release, Play-Face (non-social), Pick Up Food.

Object-Concept Series- Clutch Environment, Solitary Play, Rub Surface, Pick Up Dropped Object, Pick Up and Release, Pick Up Food.

Spatial Series- Dorsal Cling, Locomote, Climb, Stand, *<1m. Away From Mother

Locomotor Series- Hang, Locomote, Climb, Hop.

Social Series- Nipple Contact Others, Muzzle, Social Play, Dorsal Cling Others, Play Face Social, Social Clutch, Directed Aggression, Grab Object From Conspecifics, Threat, Imitate, Watch Others.

* Measure of proximity to mother, not a behavioral unit.

Stage 4

Sensorimotor- Intelligence Series- "The Coordination of Secondary Linear Schemata and Their Application to a New Situation (Parker 1977:73), Goal-Directed Activities to Social and Practical Objects (Piaget 1952).

The first really intelligent behaviors appear here, with the infant beginning to coordinate a series of familiar actions in order to achieve a goal. It displays derived secondary linear reactions (Parker 1977) by applying serial motor actions to one or more objects (or animals) such as the alternate manipulation and release of an object, pulling a food item apart with the hands, or hand to hand/hand to foot transfer of an item. Serial and simultaneous body actions also appear at this stage, which include rapid movements involving a series of motor acts or using a number of actions on the substrate.

Object-concept Series - "The Practical Object" (Parker 1977:77)

An important milestone marking the beginning of Stage 4 is the linking of visual and tactile permanence. The infant is no longer content to grasp objects but acts on them in a manner which suggests that the object can be affected by manipulation (Piaget 1954). The infant will now display a tactile search for an object outside of its perceptual field; however, any search is linked to the place in which the object first disappeared and not generalized to all situations (Piaget 1954). The young primate will now intentionally rotate and process food items like peanuts. Although the infant recognizes objects such as specific food items, at this stage it still conceives of an object linked to a particular context; for example, the grape in mother's hand is different from the grape in the food bin. "The object remains a practical object rather than a substantial thing" (Piaget 1954:65).

Spatial and Locomotor Series

The infant now greatly expands its use of space as it increasingly spends more time over a meter away from its mother. At this point, it consistently uses other animals for transportation, jumping on and off them at will while using its structural environment in a number of novel ways such as swinging from bar to bar and different styles of hanging and climbing. At first, the young animal uses the same routes to reach a goal, such as a food source, however as the knowledge of its space improves, it is able to use a variety of pathways. Often it has no apparent goal in mind and will use a number of locomotor modes for the kinesthetic stimulation.

Social Series - The First Permanent Social Objects and Independent Goal-Directed Activities to Social Objects (Piaget 1954)

For the first time the mother-infant bond is more than a physical attachment for the provision of transportation and nourishment, for although frequently moving away from her, the infant returns repeatedly to play or eat beside her. It watches conspecifics closely and extends the use of imitative behaviors to include processing and choice of food items as well as manipulation of social partners by grooming or attempting to initiate a play bout. The infant now consistently uses other animals for transport; and appears to be aware of itself as a social object that can reject, accept, or initiate a social interaction. An increase in the intensity of the infant's interactions can be observed, and it begins to act differently towards different conspecifics. It is at this stage that "fear of strangers" appears (Cowan 1978).

Metabehavioral Parameters for Stage 4

1. Type of Coordination - serial coordination of motor actions and actions with objects, trial and error coordination towards a goal.

2. Locus of Coordination - series of actions executed by self towards one or more objects , the substrate or one or more conspecifics.

3. Volition of Motor Patterns - voluntary, exerts choice.

4. Differentiation of Motor Patterns- consciously differentiated.

5. Number of Acts in Behavior Pattern - three or more acts in a behavior pattern.

6. Goal Determination - stimulus-triggered goal. Use of familiar actions to achieve the goal.

7. Context - uses new behavior patterns to act in familiar settings, also begins to move to unfamiliar settings by use of extended motor abilities.

8. Temporal/Spatial Patterning - serial application of the same and novel behavior patterns, repeat old patterns of behaviors in new ways.

9. Releasing and/or Reinforcing Aspects - pleasure in complex activity and novel experiences.

10. Sources of Stimuli - proprioreceptive and kinesthetic feedback, also feedback from social interactions.

Critical Behaviors for Stage 4

(There is an overlap in sensorimotor intelligence and object-concept critical behaviors because the idea of object-concept is linked to visual and tactile interactions with objects involving both sensory perceptions and motor systems)

Sensorimotor-intelligence Series- Rub and Eat, Simple Food Processing, Close Visual Examination

Object-Concept- Rub and Eat, Simple Food Processing, Close Visual Examination, Tactile Search, Manipulation, Self-Groom, Hand/Hand or Foot/Foot Transfer.

Spatial Series- Complex Climb, Locomotor Play, Jump.

Locomotor Series-Complex Climb, Locomotor Carry, Locomotor Play, Jump.

Social Series- Close Visual Examination Social, Rough and Tumble Play, Social Locomotor Play, Follow, Groom, Initiate Play, Fear Grimace.

Stage 5 -

Sensorimotor-intelligence Series - "Trial and Error Secondary Linear Reactions and Discovery of New Means Through Active Experimentation" (Parker 1977:75).

Actions in this stage often involve trial and error activities related to locomotion and body manipulation, and indicate the use of inventive intelligence in the young animal. The infant now begins to try different ways to process food items and to find new routes to familiar areas, as it is able to circumvent barriers between itself and its goal.

Object-concept Series - "Intermediate Object Permanence" (Parker 1977:77)

Improvements in spatial relationships allow the infant to understand sequential displacements and to find an object which it has watched being hidden, retrieved, and hidden again. The object is now perceived as being independent of the context (Piaget 1954). Search behaviors for a lost or dropped food item or a missing conspecific can now be observed; and when visiting a food source, the infant will search for a choice item instead of reaching for the first piece that comes within its grasp.

Spatial Series and Locomotor Series

The infant begins to leap from one environmental surface to another, tentatively at first, then with greater dexterity as its distance perception improves. This stage marks an advance in the concept of experimental space, as evidenced by the hesitation and apparent decision-making process before attempting a leap from one surface to another. After a few near misses, the area covered becomes greater and greater;

however, if the infant does become stranded in a precarious situation, it will contrive to use another animal to carry it back to safety. The infant is still conscious of the mother's whereabouts and will attempt to gain her attention when stranded in an unfamiliar area.

Social Series - Trial and Error Actions in a Social Context and Discovery of New Means Through Active Experimentation

This is the first appearance of inventive intelligence used in a social context. The infant begins to find ways to regain nipple contact after a maternal rejection, manoeuvre food away from another animal, or use another animal for its own purposes. The infant is now aware of itself as a causal agent that can affect the behaviors of others (Cowan 1978). The communicative ability of the infant is greatly expanded with the appearance of new gestures and facial expressions.

Metabehavioral Parameters for Stage 5

1. Type of Coordination - reciprocal, trial and error and reversing operations.
2. Locus of Coordination - a variety of actions, some trial and error, used by self towards physical and social objects, and the environmental substrate.
3. Volition of Motor Pattern - voluntary choice.
4. Differentiation of Motor Pattern - conscious differentiation.
5. Number of Acts - three or more acts in a behavior pattern
6. Goal Determination - active experimentation towards the achievement of a goal.
7. Contexts - experimentation in familiar and novel settings; expanded use of novel settings.
8. Temporal/Spatial Patterning - repetition of acts as trial and error attempts to achieve a goal and once a goal has been achieved the rate of the goal-directed activity increases. The use and orientation in space will also be greatly extended.

9. Releasing and/or Reinforcing Aspects - perceived pleasure in the achievement of a goal.

10. Sources of Stimuli - proprioreceptive, kinesthetic and social feedback.

Critical Behaviors for Stage 5

Sensorimotor-intelligence- Complex Food Processing, Visual Search.

Object-Complex- Complex Food-Processing, Visual Search, Play with Medium, Insert Item, Retrieve Item, Hand in Hole.

Spatial Series- Locomotor Games, Insert Item, Retrieve Item, Hand in Hole.

Locomotor Series- Locomotor Games, *Expanded Use of Space.

Social Series- Display, Mount, Fight, Present for Groom.

*Extrapolated from the qualitatative record of the infant's development

Stage 6 -

Sensorimotor-Intelligence Series - Achievement of Goals by Means of Mental Representations with No Experimentation Necessary (Piaget 1952, Parker 1977).

These behaviors display systematic intelligence (Piaget 1952); and are mainly geared to the acquisition of food, the use of space, and social skills. The infant now foresees the results of its actions, and acts to achieve a goal directly without experimentation; thus the goal-directed behaviors occur much more rapidly than before.

Object-Concept Series - "Object Permanence: The Representation of Object Displacements" (Parker 1977:77)

The infant is able to make deductions about the whereabouts of food items or other objects, even when it has not seen them placed. Objects are now concrete things which are the same in every situation and context. The young primate can now generalize types of food items and process them without experimentation.

Spatial and Locomotor Series - Representation of Space

The infant is now able to function efficiently within its environment. It uses all of its available space on its own without depending on its mother or other animals to transport it. At this point, the young animal adopts strategies allowing it to use its space more effectively.

Social Series - Representation and Planning Social Interactions Without Experimentation.

The infant is now able to employ tactics to manipulate social interactions. It can now act quickly to promote affiliation or avoidance of certain animals, as up to this point it has been relatively non-selective in its choice of social partner, playing with or riding on any nearby animal.

Metabehavioral Parameters of Stage 6

1. Type of Coordination - acts selectively and rapidly.
2. Locus of Coordination - self to object, object to object, self to other.
3. Volition of Motor Patterns - voluntary choice.
4. Differentiation of Motor Patterns - conscious differentiation.
5. Number of Acts - many.
6. Goal Determination - rapid and efficient achievement of goal.
7. Contexts - activities occur in all parts of the environmental setting.
8 Temporal/Spatial Patterning - novel orientations; sequences of behaviors to achieve goals become efficient and innovative.
9. Releasing and/or Reinforcing Aspects - perceived contingency control in objective activity, and novelty reinforcement.
10. Sources of Stimuli - memory images, as well as feedback from social and physical activity.

Critical Behaviors of Stage 6
Sensori-Motor Series- Problem Solving Activity.
Object-Concept Series- Problem Solving Activity
Spatial Series- Direct Choice of Appropriate Route to Circumvent a Barrier.
Locomotor Series- Direct Choice of an Appropriate Locomotor Action to Achieve the Desired Result.
Social Series- Direct Choice of Appropriate Social Action to Achieve the Desired Result.

The critical behaviors described above are broad enough to be applicable to any species of nonhuman primate; however, species-specific behaviors which meet the criteria for the attainment of any stage could be added; e.g., the double threat displayed only by cebus monkeys fits the behavioral parameters for Stage 5 and was added to the ethogram for the cebus infant.

Chapter 4. The Development of Social Cognition in an Infant Cebus Monkey

Introduction

The present research project has been designed to provide some input into the use of social cognition in nonhuman primates by investigating the development of social skills in conjunction with the development of motor and practical skills. A modification of the human-oriented Piagetian cognitive developmental model was applied to a longitudinal study of nonhuman primate infant behavior. This demonstration case study of infant development was conducted on an infant female monkey of the genus *Cebus* at the Valley Zoo in Edmonton, Alberta, Canada. The infant's mother was *Cebus apella;* however, the exact species of the infant cebus was uncertain as the female was pregnant when she arrived in Edmonton and the father was not known to the zoo administration. The infant was born on October 12 1987, into an ongoing social group consisting of her mother, two other adult females, a young adult male, and his father, a very old male.

Natural History of Cebus Monkeys

Cebus monkeys, commonly called capuchins, are members of the New World monkey Family Cebidae. They are medium-sized animals, adults weighing from 3 to 5 kgs, with the males weighing slightly more then the females (Napier and Napier 1968, Fleagle et al.1981). There are four recognized species, *Cebus albifrons, Cebus apella, Cebus capucinus* and *Cebus olivaceus*, all of which are widely distributed in Central and South America as far south as Argentina. *Cebus capucinus* is found only in Central America.

Cebus monkeys live in multi-male multi-female social groups of 8 to 30 animals, with the adult females slightly outnumbering the adult males (Napier and Napier 1968, Terborgh 1983). They are highly arboreal animals, who live in the middle and lower canopy of the forest and spend the majority of their time foraging and feeding (Fleagle et al.1981, Terborgh 1983). Although fruit and insects make up the major part of their diet, their omnivorous feeding patterns comprise a wide variety of plant parts and animal matter, which include nuts, seeds, seed pods, leaves, stems, flowers, wasps, termites, all stages of the ant life-cycle (adults, pupae, larvae and eggs), frogs, lizards, and small mammals (Izawa 1979, Terborgh 1983, Fedigan 1990). They are deliberate, manipulative, and destructive foragers; and their foraging activities include breaking branches, rooting through leaf litter, stripping bark, poking into dead trees, unfurling leaves, and cracking nuts on rocks (Moynihan 1976, Fleagle et al.1981, Fedigan 1990), Cebus monkeys employ an impressive variety of strategies to find and extract choice food items that present problems for them, such as seasonally available fruit, hard-shelled palm nuts and stinging insects (Izawa 1979. Terborgh 1983). It has been suggested that, among nonhuman primates, such complex foraging strategies are found only in cebus monkeys and chimpanzees (Parker and Gibson 1977, Boesch and Boesch 1983).

All cebus species appear to have both male and female dominance hierarchies; however, it is often the dominant male who leads the group movements, acts to protect the group and is the center of group activities. Adult males are usually very tolerant of the attentions of subadults and infants, and exhibit most of the allogrooming at resting times (Izawa 1980). Agonistic encounters between males are relatively mild, contributing to a high degree of tolerance within the group (Izawa 1980). In the wild, cebus are generally not a highly social species, spending only 2% of their total activity budget on allogrooming and other social activities (Terborgh 1983).

Cebus and squirrel monkeys outstrip all other nonhuman primates at prehending rapidly moving objects. Cebus score well on tests requiring manipulative ability, and are proficient at tasks requiring independent control of the digits (Fragaszy 1985).

Methods

The Study Group

Before describing the development of the young cebus monkey, it is important to describe the dynamics of the social group in which she was raised. The mother, who was pregnant when she arrived at the zoo, and another adult female named Cinnamon were introduced into the social group at the same time; and these two tended to spend a great deal of time together. Although the third adult female (Smokey) had been in the zoo colony for many years, she was clearly subordinate to these two females. On the rare occasions when she approached them, they would quickly move away and she was only allowed to groom them infrequently. To my knowledge, she was never the object of any grooming or affiliative behaviors from the other two females. At the beginning of the present study Jack was the only male in the group; however, when the infant was 29 weeks old, Jack's father, Hercules,a very old male, was re-introduced.It was clear from the amount of attention and deference he received that Hercules was the dominant male.

At the beginning of the study, the animals were housed in their winter quarters, consisting of an enclosure approximately 3.5 m wide by 5.5 m long by 5 m high. The room was fitted with a number of bars, a ladder, and a large plastic barrel suspended from the ceiling by a heavy chain.

Two walls of the enclosure consisted of wall-to-floor windows which allowed an observer an unobstructed view of the monkeys at all times.

The monkeys were moved to their outdoor quarters on April 18, 1988, towards the end of the infant's 30th week of life. This enclosure, which was semi-circular in shape, was much larger than the indoor facility measuring approximately 7 min diameter, 5 m in width, and 8 m in height. The entire semi-circular part of the facility was enclosed with wire mesh, again allowing the observer excellent visibility. The enclosure contained a number of structures for the use of the monkeys, including a teeter-totter, a swing, a suspended tire, and three huts on raised platforms. The huts with small heaters provided warmth and shelter. Data were taken when the zoo was closed and also when it was open to the public. The monkeys were completely habituated to public viewing and did not vary their activity patterns in any significant way when the zoo was open.

Data Collection

An ethogram (see Appendix 1) was constructed of mutually exclusive behavioral units, most of which were common to all developing infants and some of which were specific to cebus monkeys. The ethogram consists of behavioral states, which are ongoing behaviors recorded in terms of their occurrence and duration; and events which are single or transitory actions. The critical behaviors described in the previous section, which were applicable to all species, were included in the ethogram.

The observational study began on October 21, 1987, during the infant's second week of life; and continued weekly through July 1, 1988, the 38th week of life. The data were recorded using the focal animal data collection method (Altmann 1974) by means of a Realistic Miniette 19 Tape Recorder. The data were subsequently transcribed onto data collection sheets. This method of data collection was particularly useful in the present study because it provided frequencies, durations, and sequences of behavior, as well as the patterns of interactions with other member of the social group.

A total of 251 observation hours resulted in 121 hours of focal animal data, recorded in 10 minute sessions. The sessions were taken at different times of the day, depending on the activity pattern of the monkeys. In order to record the complete behavioral repertoire of the developing infant, it was important to choose a time when she was active. For this reason none of the data-taking sessions were begun when the infant was asleep.

Data Analysis

The behavioral data were entered into a computer to be sorted and analyzed to produce the following values:

a.The average weekly durations of all behavioral states, which were recorded as the average percentage of the total duration per session.

b.The average weekly frequencies of all behavioral states and events which were adjusted to be recorded as the average rate of behavior per session.

c. The average weekly frequencies and durations of the combined critical behaviors listed in Table 4.1 for each series in Stages 2 through 5, adjusted to average values per session. The combined critical behaviors for the social series were those directed to members of the social group other than the mother except where specified.

The first step in the quantitative analysis of cebus infant development was to record the beginning of each stage of development. The beginning of the different series in each successive stage was defined by the week in which the first critical behavior characterizing that stage was observed (See Table 4.1). This information was readily available from the descriptive data. The next step was to look for the concurrence or decalage of the appearance of the stages in the different series. This analysis provided a comparison of the acquisition of cognitively-oriented behaviors in social and non-social domains. The frequencies and durations of single critical behaviors were charted on line graphs to show the changes in weekly behavioral units over time. The values for the combined critical behaviors in each series in the developmental stages were also displayed on line graphs to show patterns of development in social and non-social domains.

Results

The development of the infant cebus monkey was charted not only quantitatively using focal animal data, but was described in detail in a log book. The following is a qualitative description of the young monkey's progress from a fully dependent, reflexive individual to an active participating member of the social unit. Since this is a description of the general development, and perfect synchrony of the achievement of the stages of development in all series was not the case, there is a certain amount of overlap in weeks of overall stage acquisition.

Qualitative Description of Cebus Monkey Development

Stage 1

At birth, the infant was totally dependent on her mother, suckling frequently and clinging tightly to her ventrum with both hands and feet. When the infant's head fell back periodically, she appeared to be unable to lift it back into position, inducing the mother to grasp the baby's head and replace it under her chin.By week two, the infant could change position and cling to her mother's side for periods of time. During the first four weeks, the infant's limb movements were random and undirected. Cinnamon, who normally spent time with the mother, was particularly attentive to the infant, muzzling and grooming it frequently; however, this attention did not appear to elicit any response from the infant.

Stage 2 - In Stage 2, an infant begins to exhibit more control over its motor actions and is able to coordinate some rudimentary interactions with its world, apart from the mother.

By week five, the cebus infant was able to move her head back and forth and look at her surroundings. From this time on, the infant had more control over her limbs; and began to scratch effectively and reach out to feel parts of her body. The first movement off the mother's body appeared during the seventh week; and although the infant began to crawl around on the bars, she always maintained some physical contact with her mother. At this point, periods of activity were often followed by periods during which the infant would sleep soundly while clinging tightly to the mother's ventrum whether the female was still or moving rapidly around the enclosure. When awake, the infant loosened her grip on the mother to the point where she was barely hanging on. Presaging the beginning of the next stage, the infant's interactions with the environment increased dramatically; and she began chewing and feeling everything within her reach. This could be termed an oral stage because most of the activities involved the mouth and the tongue. Although the infant was the object of the continued interest and attention of Cinnamon and Jack, her actions towards them were confined to feeling, licking, and chewing.

Stage 3 - Behaviors at this stage are characterized by the coordination of vision and prehension, and by the beginning of the ability to perceive the permanency of objects. The concept of an object in Stage 3 is firmly linked to the actions that the infant directs towards that object. If there is no act of accommodation towards the object, it does not exist for the infant (Piaget 1954).

The cebus infant reached Stage 3 in the social series a full week or more before achieving this stage in the non-social series. The first social play face appeared in the seventh week, and the improved hand-eye coordination was evident in the clutching and grabbing actions directed towards Jack and Cinnamon. It was not until the end of the eighth week that the infant began to clutch the bars and other objects in the environment without groping. This ability improved rapidly over the next few weeks; and, although the infant still had not left her mother completely, she was extremely active, moving about and clutching at everything within her reach.It was not until the ninth week that the young cebus began to ride dorsally on her mother, and started to reach for bits of food from her mother's hand and from the the bars. This was the first indication of rudimentary foraging and feeding on solid food. From this time on, the infant rode almost exclusively on her mother's back. It was interesting to note that a return to the tight dorsal cling occurred only when the mother was moving on the floor. Indeed, until the infant was well into Stage 5, she showed a great reluctance to approach the floor.

The subordinate female, Smokey, who until this point had rarely approached the mother, began to spend time muzzling the clinging infant. The infant seemed to act as a social mediator, because Smokey appeared to be able approach the mother at will when the infant was present. Social play between the infant and the mother and Cinnamon began at week 11, and the first move from bodily contact with the mother appeared at week 12. The mother had been actively restraining her infant during the previous weeks, but finally let her move away a few inches in the safety of the barrel. This week seemed to be a milestone in her young life because, once off her mother, she greatly expanded her social and physical horizons. She moved onto Jack's body for a few moments, and began to experiment with more complex motor actions.

Motor and social development progressed rapidly from this point. The infant began to ride dorsally on the other animals more frequently and was successful in her attempts to get food from them. She began to climb and run along the bars, tentatively at first, but she quickly became more confident and secure in her locomotor ability. Other locomotor and postural actions followed, and soon definite patterns of activity were observed; e.g., social approach and retreat. The expanded use of locomotor actions coincided with the movement of the infant over 1 m away from her mother in the last weeks of Stage 3.

Stage 4 - The main cognitive advance in this step is the ability to coordinate a number of familiar actions in order to achieve a goal, and the appearence of purposeful actions.

At this stage, the mother was far less restraining and began to leave the infant, who often followed her. Intentional social activities became much more apparent, with the infant crawling all over Cinnamon and Jack and attempting to initiate play bouts. The mother's actions with food items were watched very closely and often repeated (imitation?). The infant, now very proficient at climbing and running along the bars, was spending longer periods away from her mother.

The 18th week, the beginning of Stage 4 in all series, appeared to be a landmark in the infant's locomotor development, as she began to use set patterns of locomotion and set routes to achieve an intended destination (food source or mother). This week also was the first time the infant actively manipulated padlocks and other environmental objects. The first attempts at grooming appeared at this point; and the infant appeared to be more confident in her social interactions, ignoring or actively rejecting some social advances.

As this stage progressed, the pattern of climbing became more complex, and different postural attitudes appeared. Late in Stage 4, the ability to leap from one bar to another marked a major accomplishment which greatly expanded the young monkey's use of space.

Stage 5 - This stage marks the beginning of inventive intelligence to achieve a goal, often involving the use of trial and error behavior patterns.

In the early weeks of Stage 5, the ability to jump from one environmental surface to another appeared to be a mixed blessing for the infant. She frequently found herself stranded on an unfamiliar bar, and appeared to be uncertain about the return route. In this situation, she would jump on a nearby animal and allow it to take her to a familiar area, often near the mother. The locomotor and spatial abilities rapidly progressed to the point where the infant abandoned her earlier familiar paths and began using a variety of different,more extensive routes. The infant did not venture onto the floor until the beginning of Stage 5, even though food was often placed there. The infant's foraging strategy on the floor was quite different from that used on the bars or in the barrel. She often spent significant periods of time in the barrel, picking up food and eating it, while on the floor she would pick up the food on the run and eat it on a familiar perch on the bars.

Once manipulatory actions became part of the infant's behavioral repertoire, she began to process food items in a number of different ways, depending on the properties of the food. Rather than picking up the first item encountered, the young monkey spent time searching through the food bin for a specific item. The appearance of preferential activity was also evident in the social domain, as Smokey seemed to be the animal of choice for transportation, while the other members of the social group were the targets for infant's greatly expanded social actions such as chases, wrestles, and invitations to play. Grooming was confined to the mother during the first weeks of Stage 5.

At week 27, the infant began to use a greater number of behavior patterns which could be construed as intentional in social and non-social areas. The first "present for groom" appeared; and the infant began wedging bits of food in different locations, only to return later to retrieve and eat the food.

The monkeys were moved outside when the infant was 29 weeks old, an event which greatly expanded her use of the environment. She was exposed to a number of new structures and new natural objects such as leaves and insects. Also a new conspecific. Hercules, an old adult male, was introduced into the social group at week 30 an event which elicited the first "fear of strangers" behaviors. Although the young monkey directed a number of fear grimaces, teeth grinding, and hand wringing behaviors towards the old male, she did not avoid him, but seemed actively to seek his attention. From this point, the use of facial expressions increased; and on week 33, the first double-threat, specific to cebus monkeys, was observed. Grooming and other social activities with group members other than the mother became a more significant part of the infant's activities.

Locomotor "games", consisting of a number of motor actions repeated in the same sequence over and over again on the teeter-totter and other structures, appeared at week 35. From this point until the end of the study (week 38) these games and locomotor play became the major activities of the infant; and although she continued to interact with the other animals, the time spent in social activities diminished.

Throughout the study, the only problem-solving activity observed was in week 35 when the infant attempted to get a piece of fruit resting outside of the enclosure. She was unable to reach it by extending her hand through the mesh; and after attempting a number of maneuvers, finally lay on her stomach parallel to the mesh, slid her arm under it, extending her reach and enabling her to retrieve the fruit. Towards the end of the study, the infant began to practise some rudimentary social manipulation on her mother, who was beginning to be ambivalent towards her. When the mother ignored the infant's presenting for groom, she would move directly towards the mother's nipple, an action which invariably elicited the desired bout of grooming.

Stage 6 - Stage 6 behavior patterns indicate the ability to use mental representations in the young individual's interactions with its social and physical environment. New situations are responded to quickly, indicating the ability to use prior knowledge to predict the outcome of an action.

The young cebus did not exhibit any behaviors that could be characterized as indicative of the use of a mental representation although she was only nine months old at the end of the study. Spinozzi's (1989) study of cebus development indicated that her subjects had not attained Stage 6 in the object-concept series, even after two years. Although other researchers have attributed Stage 6 capabilities to cebus monkeys (see Natale and Antinucci 1989d for a review), Spinozzi's research indicated that cebus monkeys never did develop the capacity to represent an object mentally.

Quantitative Analysis of Cebus Monkey Development

The quantitative results focussed on the development of social cognition in comparison to the development of non-social areas of intelligence. The data were also used to investigate nonhuman infant development in sensorimotor, object-concept, and spatial cognition, as well as locomotor skills. The premise, when using a Piagetian model to investigate the development of early intelligence, is that each stage is more complex in both motor and cognitive function than the previous stage, with each stage being characterized by the same behavioral parameters.

One objective was to record the weeks of life in which the critical behaviors first appeared, allowing a description of the age of acquisition of each stage of development in the different series (see Table 4.1). The young monkey achieved Stage 2 from weeks five to seven, advanced to Stage 3 behaviors from weeks seven to twelve, reached Stage 4 at week 18, and Stage 5 from weeks 20 to 35. Piaget (1952) found synchrony in the acquisition of the stages of development in the different series for human infants. However, in the infant cebus monkey, synchrony was evident only in the fourth stage. The Stage 3 socially-directed critical behaviors appeared slightly before the sensorimotor and object-concept series and over a month before the locomotor series. Stage 5 locomotor behavior patterns did not appear until well after those in the other series were well established (Figure 4.1.).

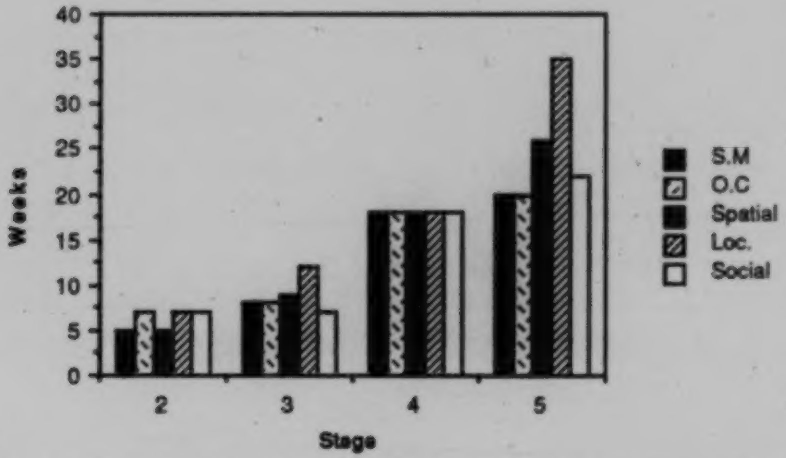


Figure 4.1. The weeks of acquisition of the stages of development in the different series.

The decalage in locomotor behaviors is not surprising in an arboreal species, since the the more complex motor activities characterizing Stage 3 (climbing, running, and walking on the substrate well above the ground) all require good control of hand-eye coordination. The mother was also a limiting factor in locomotor activity, since the infant was able to expand her locomotor skills only after first leaving contact with the mother at 10 weeks of age and subsequently moving over 1 m away at 14 weeks. Maternal restraints, which began at nine weeks, also kept the infant from locomoting freely.

The values used in this part of the analysis were the average weekly frequencies, which will be referred to as rates, and durations per session of the combined critical behaviors defined in Table 4.1 for each series in Stages 2 through 5. The Stage 1 behaviors were not listed as they were not used in the analysis. The overlap in the critical behaviors described for some of the series (see Table 4.1.) is indicative of their application to different aspects of behavioral development. This overlap is particularly evident in the sensorimotor-intelligence and the object-concept series, since the perception of the permanence of objects is so vital to the understanding of their relationship to the developing individual. Clearly the spatial and locomotor series are also closely related, since an infant must develop spatial knowledge before it can successfully operate in the environment.

Before discussing the stage by stage development of the cebus infant, one observation should be made regarding the changes over time in the average weekly rates of all behaviors compared to those of the combined critical behaviors. The most striking feature of the quantitative analysis was the fact that although the rates of all behaviors gradually increased in a linear fashion (Figure 4.2), the rates of the critical behaviors in the respective series increased in a more sporadic fashion punctuated by peaks and low points (Figures 4.3., 4.4., 4.7., and 4.8.).

Stage 1

Since the present study was directed primarily towards the development of social cognition and was interested specifically in charting the progression of social behaviors *directed* by the infant towards members of the social group other than the mother, the durations and rates of Stage 1 behaviors were not used in this analysis. During this stage the infant monkey was clinging tightly to her mother; and although she was the object of interest and social actions from the other animals, she was not responsive to these advances.

Table 4.1. Critical Behaviors for Developmental Stages 2 to 5

Stage 2	Stage 3	Stage 4	Stage 5
Sensorimotor-intelligence Series			
Suck Thumb Dir.	Clutch Environ.	Rub & Eat	Compl.Fd.Proc
Scratch Dir.	Rub Surface	Simple Proc.	Visual Search
Look Around	Eat Solid Food	Close Visual-Examination	
Loose V.Cling	Pick up & Rel.		
Feel Environ.	Play Face-Non-social		
Feel Body Part	Pick up Food		
Object-Concept Series			
Feel Environ.	Clutch Environ.	Rub and Eat	Displace
Lick Surface	Solitary Play	Simple Proc.	Compl.Fd.Pro
Chew Surface	Rub Surface	Tactile Search	Vis.Search
Chew Body Part	Pick up & Rel.	Manipulation	Play Medium
Feel Body Part	Pick up Food	Self-Groom	Insert Item
	Drop and Pick Up	Close Visual-Examination	Retr.Item
		Hand/Hand Transfer	
Spatial Series			
Loose V.Cling	Dorsal Cling	Complex Climb	Loc.Games
Look Around	Stand	Locomotor Play	Plan Loc.
Feel Environ.	Locomote	Jump	Insert Item
Lap Sit Mother	Climb	Reverse Field	
Sit Beside Mo.**	Away from Mo.<1m.**		
Away from Mo >1m.**			
Locomotor Series			
Crawl on Environ.	Hang	Complex climb	Loc.Games
Crawl on Other	Locomote	Locomotor carry	Plan Loc.
Circle Mother	Climb	Locomotor play	
	Hop	Jump	
Social Series			
Feel Cagemate	Nip.Contact Oth.	Groom Mother	Display
Lap Other	Crawl on Other	Groom Other	Mount
Chew Other	V.Cling Other	Vis.Exam Other	Fight
Lick Other	Muzzle	Loc. Play(Soc)	Pres.Grm
	Social Play Mo.	R.& T.Play	Dbl.Thr***
	Social Play Oth.	Follow	
	Dorsal Cling Oth.	Initiate Play	
	Play Face(Soc.)	Seek Nip.Other	
	Social Clutch	Fear Grimace	
	Dir.Aggression		
	Grab Object from Other		
	Threat		
	Imitate		

** Measures of proximity to mother, not behavioral units

*** Behavior specific to cebus monkeys

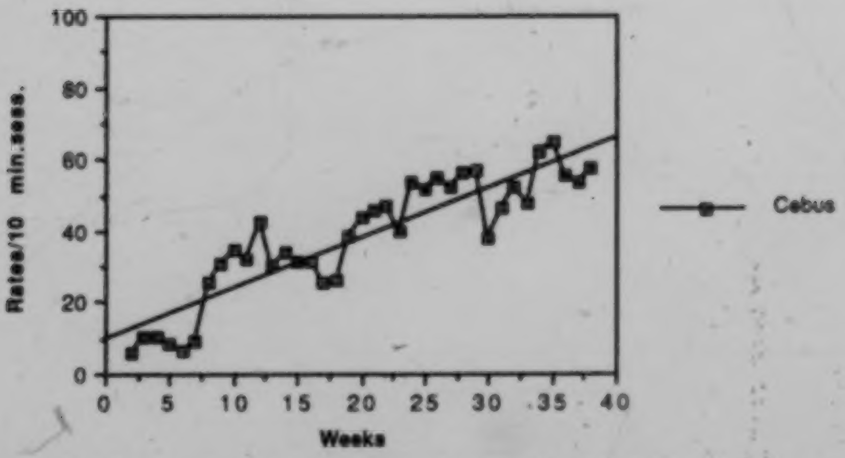


Figure 4.2. The average weekly rates of all behaviors over the 38 week study

Stage 2 (Figure 4.3)

Sensorimotor-intelligence Series - At week 5, the first Stage 2 activities appeared as the infant was able to bring her reflex actions under greater motor control. The early interactions with the environment, once acquired, became an important part of the infant's activity patterns and remained so for the duration of the study.

Object-concept Series - During Stage 2, the infant showed some interest in objects in the environment, however most of these were orally-oriented. The use of these behaviors diminished after Stage 4 had been reached long before the end of the study .

Spatial Series - One of the first signs of spatial orientation in Stage 2 was the appearance of attention directed to the environment, as infant began to look around at week 5. This major achievement was reflected in the high levels of spatial activities in the early weeks of Stage 2, Spatial knowledge continued to improve throughout this stage due to the movement of the infant off her mother's body at week nine.

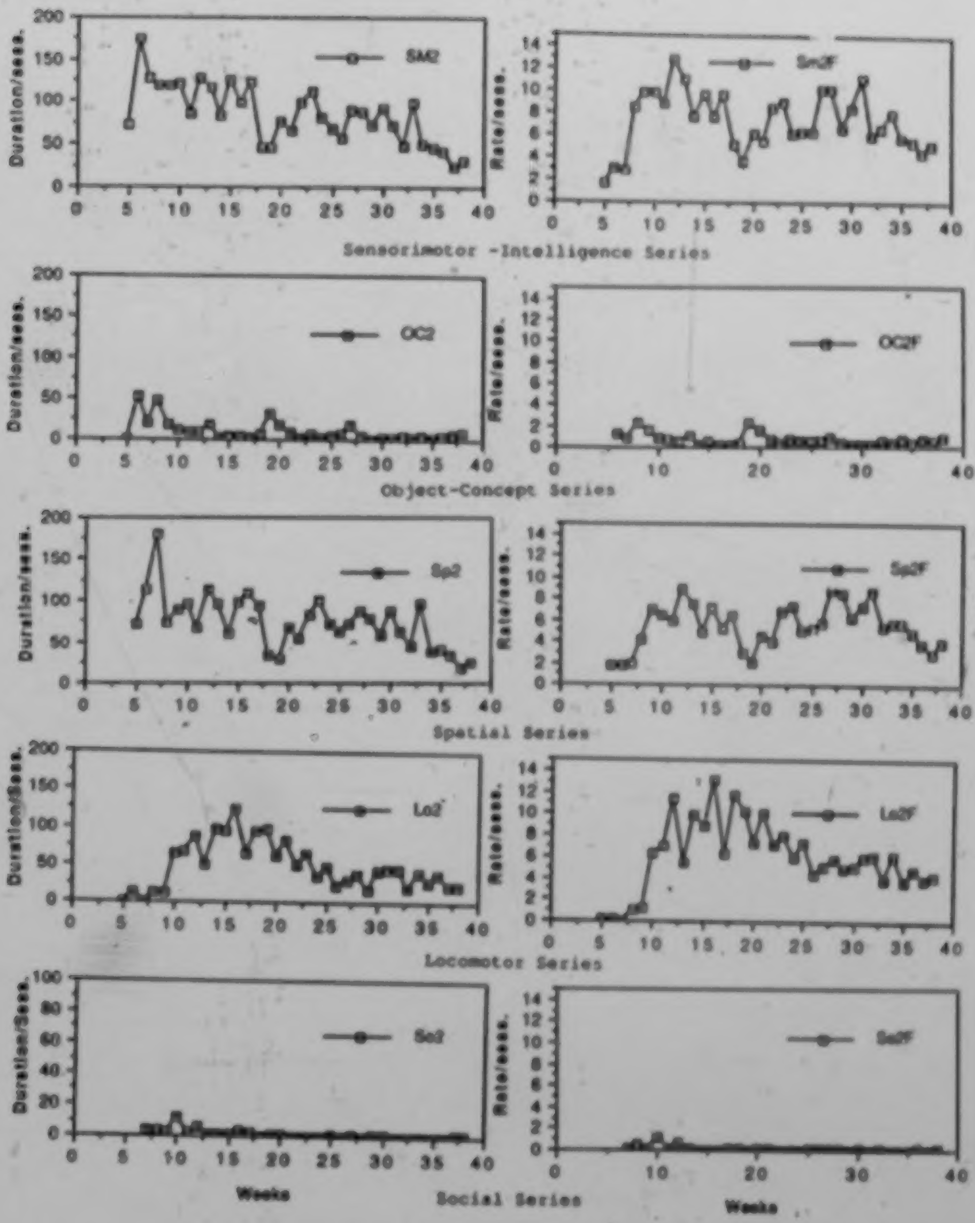


Figure 4.3 The average durations (in seconds) and rates per 10 minute session of the combined Stage 2 critical behaviors of the cebus monkey

Locomotor Series - Stage 2 locomotor activities were confined to crawling on environmental surfaces. The incidence of crawling increased dramatically when the infant moved off her mother's body at week 12.

Social Series - The cebus infant was not a socially-oriented animal in Stage 2. She began to feel and chew the other animals for short periods of time when they approached her. Since she did not even begin to move away from the mother until the end of Stage 2, her mother was still the focal point of her world. There was a slight peak in the duration and rates of Stage 2 socially-directed behaviors at week 10, after the infant had begun to ride dorsally on her mother. Although the infant continued to use Stage 2 behaviors in the sensorimotor-intelligence, spatial, and locomotor series until the end of the study, few Stage 2 social behaviors were exhibited after the 15th week of life.

The principal achievements in Stage 2 were spatially-oriented (looking around at the environment), locomotor actions (crawling), and sensorimotor movements related to the infant's own body. The random movements characteristic of Stage 1 were now coming under better motor control. The general trend over the duration of the study in Stage 2 behaviors was a high point at the beginning, followed by an overall "unsteady" decline marked by peaks and low points in durations and rates. This decline was much more evident in the object-concept and the social series. Since the infant was not locomoting independently, staying within 1 m of her mother until week 12, the scope of locomotor activities at this stage was limited to crawling around the bars within reach of the mother.

Stage 3 (Figure 4.4.)

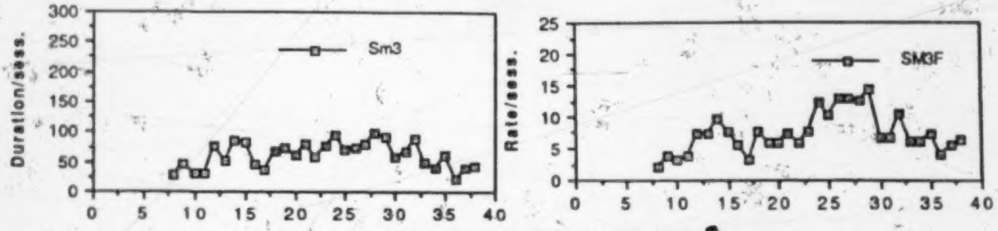
Sensorimotor-intelligence Series - These actions figured prominently in the Stage 3 behavior patterns, due primarily to the newfound ability to clutch environmental objects, and the beginning of the ability to understand that the objects that were acted upon had some permanency. The infant began to eat solid food in Stage 3, which was included in her sensorimotor activities. This would likely explain the relatively consistent average duration of this series throughout the remainder of the 38 weeks.

Object-concept Series - The behaviors that presage the concept of object permanence, and which are so important to an infant's understanding its physical world, were beginning to appear. The infant began to direct her actions towards objects in the enclosure; and was able to grasp these objects and the bars with greater accuracy, and thereby begin to gain knowledge of her surroundings. These early interactions with the environment marked the awakening of the idea that objects exist outside of the infant's visual range.

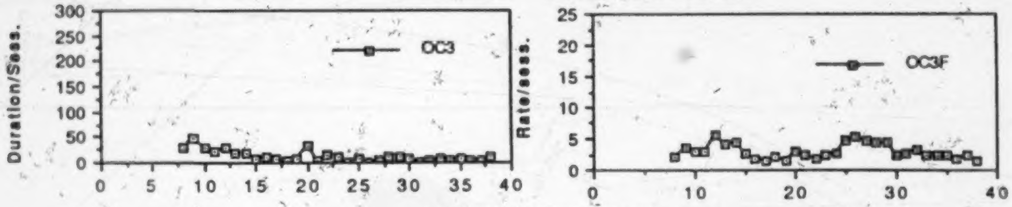
Spatial Series - The infant began to ride dorsally on her mother at this stage, a development which greatly enhanced her knowledge of her world. The overlap in spatial knowledge and locomotor ability can be seen in the similarity of the rates of spatially-oriented and locomotor activities.

Locomotor Series - It should be noted (see Table 4.1.) that the critical locomotor behaviors in this stage make up the major proportion of an arboreal monkey's motor repertoire. The first expression of Stage 3 locomotor behavior patterns coincided with the movement of the infant over 1 m away from her mother after week 12, several weeks after the onset of the other series when the ability to coordinate prehension and vision was well established. The Stage 3 locomotor behaviors included running, walking, and climbing, actions which were to form the basis for a very large proportion of the adult cebus monkey's locomotor activities. It is not surprising that these Stage 3 locomotor behavior patterns continued at a relatively high rate throughout the study.

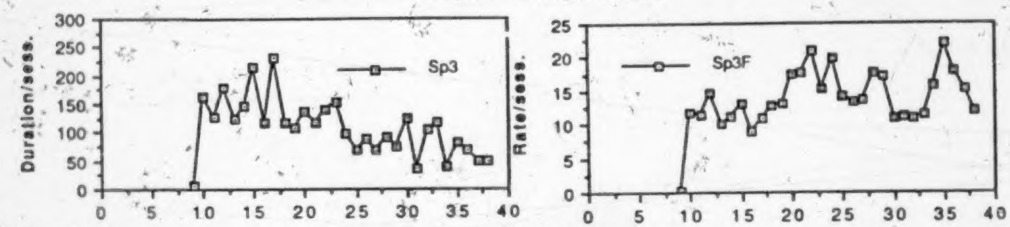
Social Series - Stage 3 socially-directed critical behaviors began at week seven, a full week before the activities in the sensorimotor, object-concept and spatial series, and five



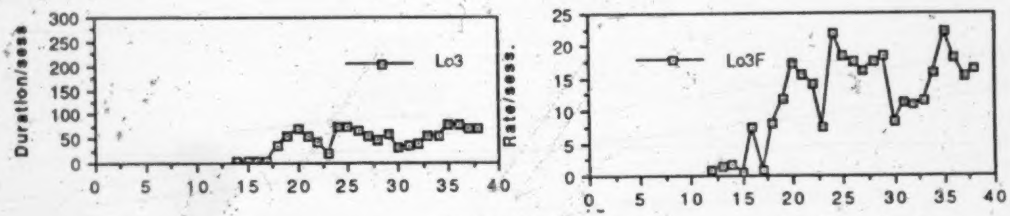
Sensorimotor - Intelligence Series



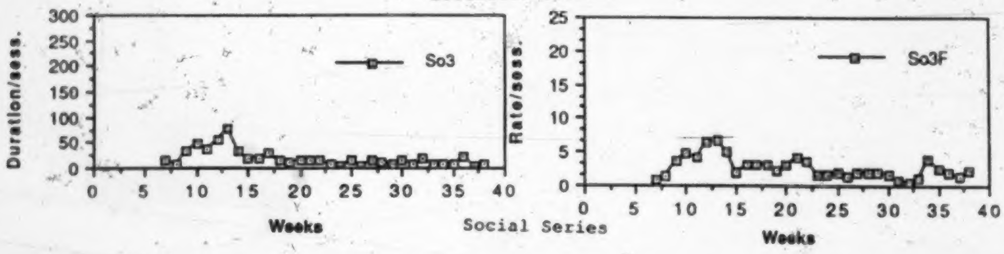
Object-Concept Series



Spatial Series



Locomotor Series



Social Series

Figure 4.4. The average durations (in seconds) and rates per 10 minute session of the combined Stage 3 critical behaviors of the cebus monkey

weeks before Stage 3 locomotor actions. During the first weeks of the infant's Stage 3 social activities, the infant was still maintaining contact with her mother. Stage 3 social interactions peaked in duration at week 14, just before the infant began actively using Stage 3 locomotor behaviors, then dropped abruptly as the activity pattern shifted to a more locomotor mode (Figure 4.5).

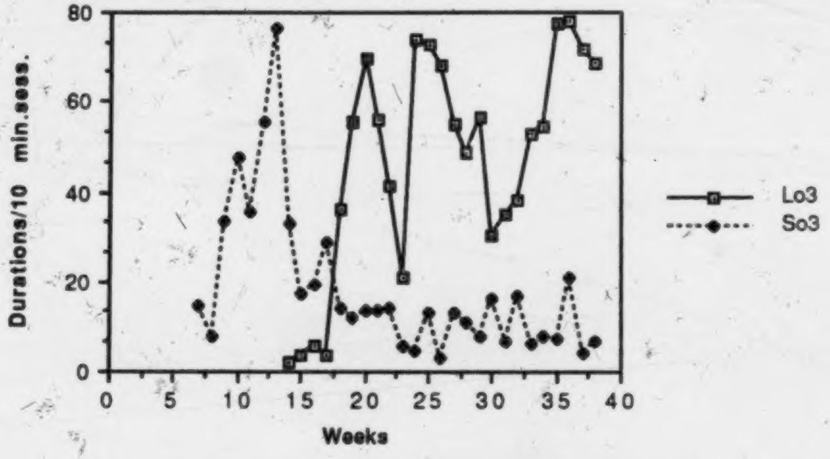


Figure 4.5. The average duration in seconds per 10 min. session of Stage 3 locomotor and social behaviors.

At this point, the infant's newly developed locomotor activities and expanded spatial horizons began to take over the major part of her activity budget. Except for the spatial series, which included the time spent clinging dorsally to the mother, the social behaviors were prominent in the early weeks of Stage 3.

The average durations of time spent per session in Stage 3 object-concept and social behaviors declined to a very low level after week 20 (Figure 4.6), while Stage 3 behaviors in the spatial and locomotor series, particularly, remained a significant part of the infant's behavioral repertoire until the end of the study (Figure 4.5).

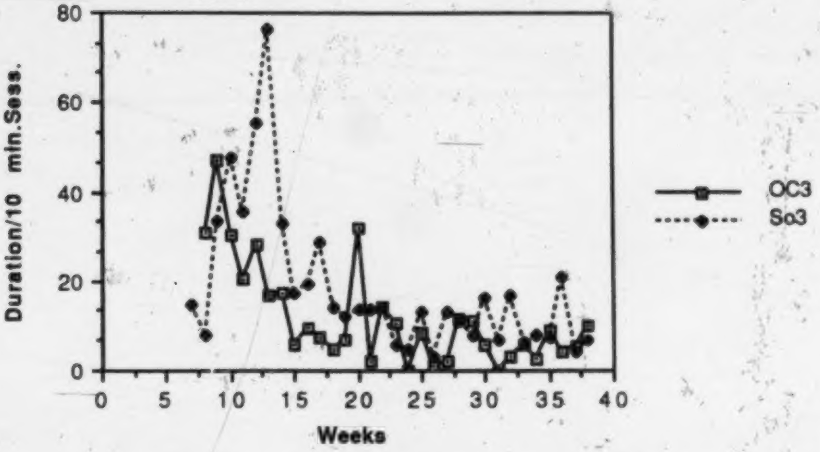


Figure 4.6. The average duration in seconds per 10 min. session of Stage 3 object-concept and social behaviors

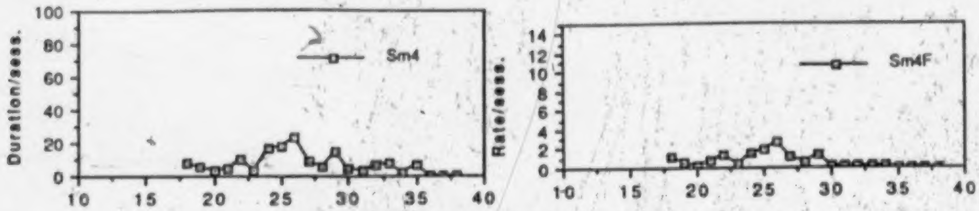
Stage 4 (Figure 4.7)

Perfect synchrony was observed in the achievement of Stage 4 critical behaviors in all series at week 18.

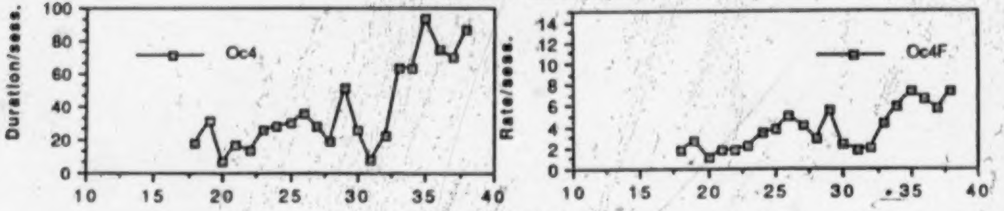
Sensorimotor-intelligence Series - These Stage 4 behaviors were limited to the first appearance of the ability to process food items. The use of these behaviors peaked at week 25; then were replaced by the more selective Stage 5 food-processing abilities.

Object-concept Series - The infant steadily improved upon her abilities to manipulate environmental objects. Object-concept behaviors took priority in the infant's life; and her understanding of the permanence of objects, although not yet complete, was now independent of her "sphere of activity" (Piaget 1954:41). These Stage 4 behaviors continued to take up most of the young animal's time for the rest of the study.

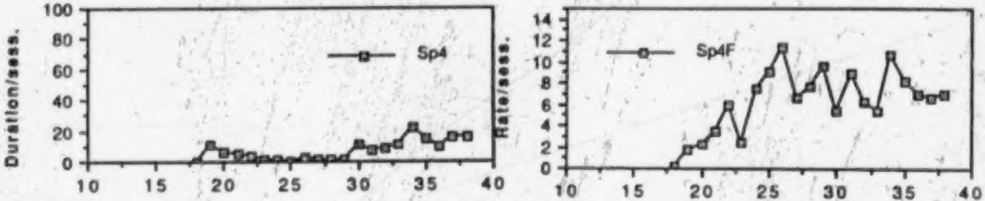
Spatial and Locomotor Series - At the Stage 4 level, the behavior patterns in both series were similar, as spatial cognition and locomotor skills became almost inseparable. Despite the relatively low duration of time spent in Stage 4



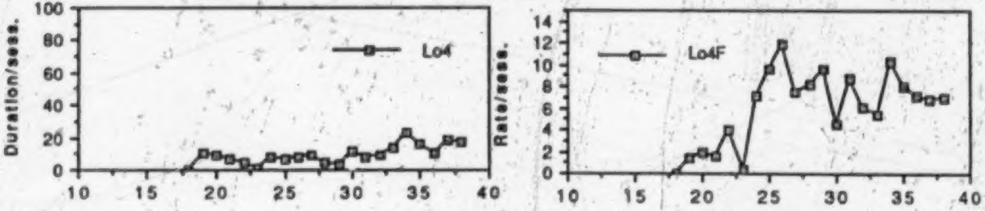
Sensorimotor -Intelligence Series



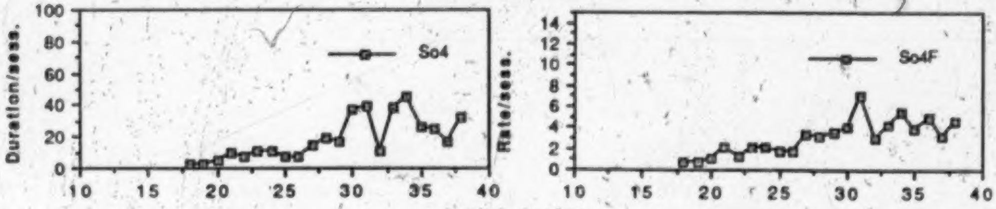
Object-Concept Series



Spatial Series



Locomotor Series



Social Series

Figure 4.7. The average durations (in seconds) and rates per 10 minute session of the combined Stage 4 critical behaviors of the cebus monkey

locomotor and spatial behaviors, the rates of these behaviors remained at a high level compared to the other series. This likely reflects the fact that the ability to jump through space from one bar to another, an action which has no duration, began at this point. Once perfected, the infant continued to use this ability frequently to expand her locomotor activities and use of space.

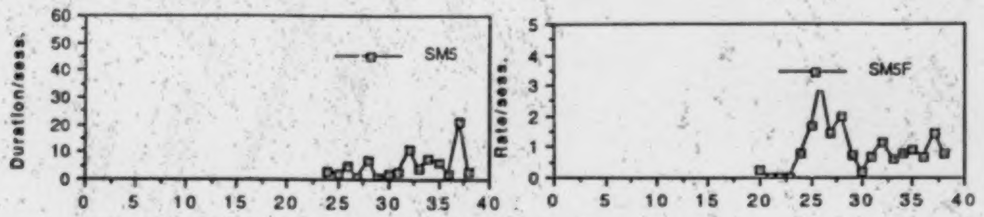
Social Series - The average duration and rates per session of Stage 4 social behaviors increased slowly beginning at week 18, then rose sharply after the infant was moved outside and exposed to a new conspecific, the old male. It appeared that the cognitive abilities related to intentional interactions with the social and physical environment had come to the fore.In terms of the duration of time spent in Stage 4 activities, social interactions ranked second only to object-concept behaviors. The infant was now beginning to try to influence her conspecifics by her actions; e.g., initiating play, grooming etc.

Stage 4 sensorimotor-intelligence, spatial, and locomotor behaviors formed a relatively insignificant part of the infant's activity time-budget compared to object-concept and social activities. However, with the exception of the sensorimotor-intelligence series, the infant continued to exhibit relatively high rates of Stage 4 behaviors in all domains.

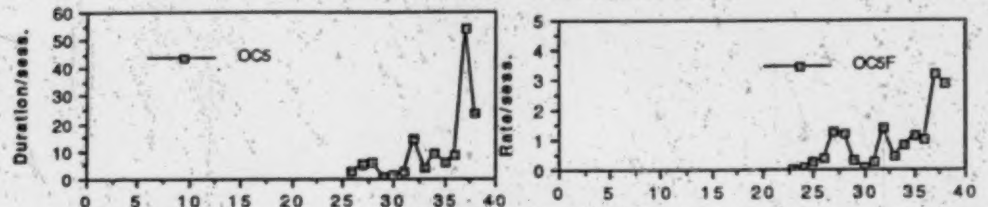
Stage 5 (Figure 4.8.)

Sensorimotor-intelligence Series - The range of Stage 5 behaviors in this series was limited to complex food processing and searching for particular food items. The rates of these behaviors reached a relatively high level when first acquired, but did not figure as an important part of the infant's activities thereafter.

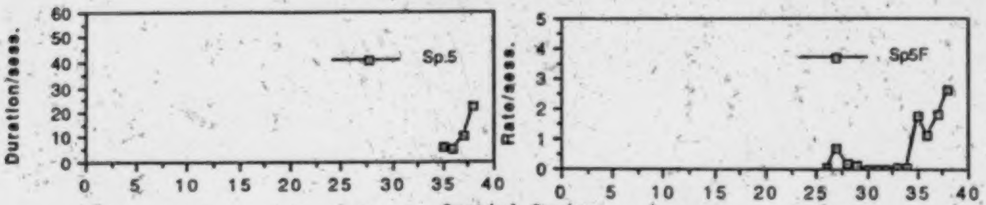
Object-concept Series - Stage 5 object-concept behaviors reflected the young cebus monkey's penchant for manipulating objects in the environment. Once achieved, the use of these



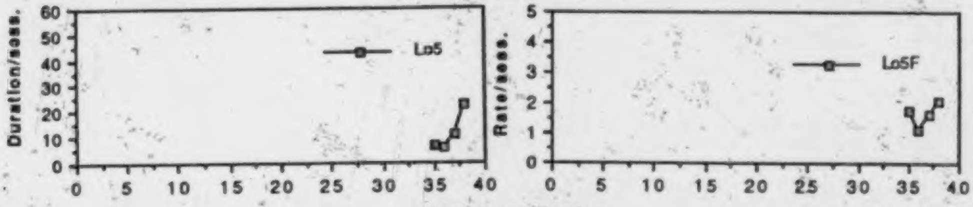
Sensorimotor -Intelligence Series



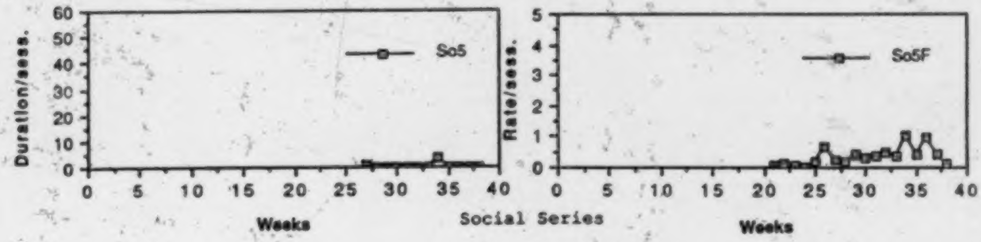
Object-Concept Series



Spatial Series



Locomotor Series



Social Series

Figure 4.8. The average durations (in seconds) and rates per 10 minute session of the combined Stage 5 critical behaviors of the cebus monkey

behavior patterns remained high in duration and frequency, relative to the other series.

Spatial and Locomotor Series - At this stage of development, although there was a spatial component in her ability to hide things, it appeared that the spatial cognition of the young monkey was used primarily in a locomotor sense (see durations of spatial and locomotor behaviors). The achievement of Stage 5 locomotor critical behaviors lagged behind the other series; but once the infant began to take part in locomotor games and solitary locomotor play, the duration and rates of this series increased abruptly.

Social Series - Stage 5 social behaviors were not prominent in the infant's behavioral repertoire, although she continued to direct Stage 4 social behaviors at a high level, relative to the other series, until the end of the study. The small peak in the duration of these social patterns was concentrated in the 34th week. The rates were much more consistent given the fact that Stage 5 social activities include fights, mounts, and displays that are of very short duration in a young monkey. When the use of complex locomotor behaviors escalated at week 35 and the Stage 5 object-concept behaviors became an integral part of the infant's behavioral repertoire, the Stage 5 social behaviors declined and almost disappeared. (Figure 4.9).

Summary

Although the values for each of the five series were charted and discussed, the most salient comparisons of cognitive development would seem to be with the object-concept, locomotor series and social series where there is little overlap in critical behaviors.

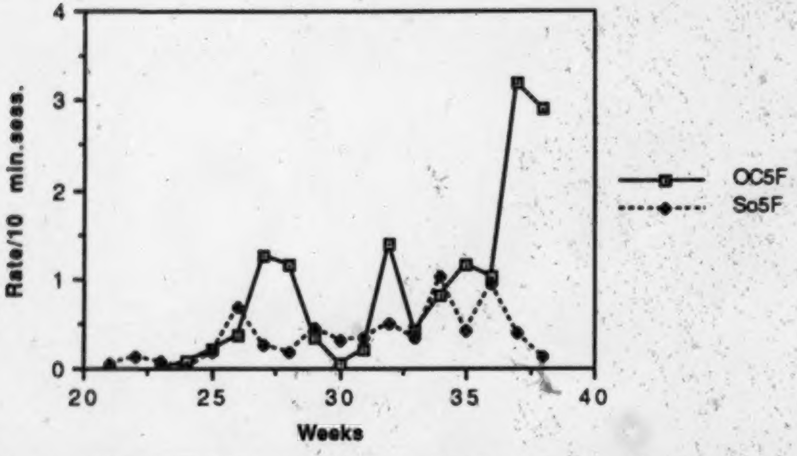


Figure 4.9. The average rates of per 10 min. session of critical object-concept, locomotor and social behaviors in Stage 5

In Stage 2 there was little expression of socially-directed behaviors. The fact that this behavior was accompanied by relatively low values in the object-concept series is an indication that this lack of sociability is related in part to the infant's inability to perceive the permanence of objects in both the physical and social world. An infant's perception of objects at this stage of development is limited to situations in which the objects can be seen. This limitation can be readily observed when the infant does not look around if an object disappears from view, and does not appear to notice if another animal has moved from its line of vision. Another contributing factor to the lack of socially-directed actions could be that the arboreal life-style of cebus monkeys does not allow the very young members of the social group to locomote independently until they are fully capable of hand-eye coordination. It is important to note here that once Stage 3 was attained, with the appearance of the rudimentary ability to coordinate prehension and vision, this ability was first used in a social context. Stage 3 locomotor behavior patterns, which were destined to make up the large proportion of her subsequent movements, were only evident after the hand-eye coordinations were well established, fully five weeks after the infant had achieved Stage 3 in the social domain.

The lack of synchrony in the development of the respective series in Stages 2 and 3 reflects the fact that the infant was still spending a great deal of time on the mother or in close proximity to her. By Stage 4 the infant was fully independent in a locomotor sense, allowing the attainment of these behavioral patterns to develop simultaneously with those in the other series. The dramatic delay in the appearance of Stage 5 locomotor actions was likely indicative of the continuing reliance the young monkey placed on Stage 3 locomotor patterns.

Stage 3 was the first truly social stage in the young cebus monkey's life. The critical behaviors in the social and object-concept series both increased after the infant began riding on her mother's back, facilitating interactions with the environment and greatly expanding the infant's spatial and social horizons. With the acquisition of Stage 3 capabilities, the infant was able to direct a whole range of new social behavior patterns towards other animals when they approached, and thereby begin to grasp the first inkling of the fact that her cagemates were a permanent part of her world. It is interesting to note the extent of Stage 3 critical behaviors in the social series compared to those in the other domains (see Appendix 2). Stage 3 social behaviors peaked in duration and rates at week 14, then began to decline when the Stage 3 locomotor activities began to increase and the infant approached Stage 4 (Figure 4.5). The same pattern of decline was observed in the object-concept series (Figure 4.6). The Stage 3 behavioral patterns in both these areas were often used in a practical sense, to pick up food from the substrate or take it from a conspecific. These behaviors were replaced by the more-cognitively oriented Stage 4 actions by week 18.

The social and object-concept activities that were retained in the behavioral repertoire until the end of the study were the Stage 4 patterns, which according to Piaget (1952) is the stage in which the first really intelligent behaviors appear. At this point the infant was beginning to coordinate a series of familiar actions to achieve a goal. She was actively moving about on the other animals, primarily Cinnamon and Jack, attempting to initiate play, beginning to groom, and using mildly aggressive actions to reject social advances. Stage 4 marked the beginning of close visual examination, of the mother and the other animals, and it appeared that the infant was imitating or learning new manual techniques by observation. The infant began manipulating padlocks and other available objects using a series of different actions, as well as using some of the adult's actions to process food items.

Although Stage 5 locomotor patterns did not figure significantly in the infant's overall activities, at this point she greatly expanded her spatial horizons and began using the entire enclosure, including the floor. Stage 5 marked the first appearance of inventive intelligence used in a social context. The infant began to use other animals as transportation to and from an inaccessible bar and tried to manipulate her mother's actions. She also began to direct specific types of interactions and act selectively towards different animals. While Cinnamon and Jack were the objects of her playful advances, the young monkey spent twice the time riding on the subordinate female than on the other two animals combined. At this point, the infant was introduced to her first stranger, an old male, and showed very ambivalent actions towards him. She approached him frequently while displaying fear grimaces and typical cebus fearful behavior patterns; e.g., teeth grinding and hand wringing (Oppenheimer 1973). Although the young monkey was able to demonstrate the use of Stage 5 social behavior patterns, the majority of the actions directed to conspecifics were at the Stage 4 level of complexity.

Stage 5, according to the Piagetian model, is characterized by trial and error actions used on environmental objects and the discovery of new means through active experimentation (Piaget 1952). These behavior patterns were very obvious in the object-concept series, as the infant began trying different approaches to process food items depending on their properties, and operating on the environment in new ways. After week 22, the Stage 5 object-concept behaviors really took over the infant's experimental behavioral repertoire, although locomotor games became a significant part of the activity pattern. Stage 5 social behaviors, which had not figured greatly in the infant's activities, had diminished to a very low level by the end of the study.

Conclusions

Clearly a statistical approach to a developmental study such as this would be inappropriate with a sample of one individual, and any statements made using the data as being representative of cebus monkeys in general would have to be carefully considered. However, it should be emphasized that this is a demonstration project and as such has two important contributions to offer:

1.The model and method of analysis can be useful in the investigation of infant development in any nonhuman primate species, whether the animals are in a semi-free ranging, wild, or captive social group. The information gained should provide the opportunity to compare developmental trends in social and non-social domains, taking note of the effects of the rearing environment and contextual factors.

2. Although the actual ages of attainment of the stages of the development may vary between individuals, certain basic developmental patterns that were observed could be expected

to remain constant over all infants in any particular species.

The patterns observed in the longitudinal study of the cebus infant that appear to be basic to cebus monkey development are as follows:

a. There is an obvious decalage or lag in the development of Stage 3 locomotor behavior patterns, which are the actions that make up the bulk of the cebus monkey's locomotor repertoire. This lag reflects the importance, in an arboreal species, of well established hand-eye coordination before an infant can move away from its mother and begin independent locomotion.

b. The dramatic increase in Stage 3 spatially-oriented behaviors and basic locomotor patterns after the infant became confident of her abilities was associated with a decline in the other Stage 3 activities. This pattern of development can likely be observed in other arboreal species. Sensory stimulation is produced by novel events, increased stimulus intensity, and increased stimulus complexity, with the sensory input coming from internal (proprioreceptive) stimuli or external stimuli from the environment (Baldwin and Baldwin 1977). The added sensory input from the use of a number of new and different locomotor techniques in new and different areas would surely result in the continuation of these activities at a high level. The stimulation from the early social interactions would likely have diminished by the time the infant was locomoting independently.

c. Development in the object-concept and social series in Stages 2 through 4 show the same general trends in the acquisition and use of the critical behaviors. These series indicate the infant's progress in the development of the ability to perceive the permanence of objects in its physical and social world. The acquisition of this concept is one of the major accomplishments of infancy, and is vital to an individual's ability to deal with the environment (Lefrancois 1989). In human developmental studies these abilities are referred to as object and people permanence (Smith 1989). In Stage 2 the infant is not aware of the constancy of objects or other animals, and consequently does not seek out interactions with the physical and social environment. The majority of Stage 2 actions directed towards the environment are of an oral or tactile nature, and their scope is determined by the location of the mother. When this ability begins to appear in Stage 3, the concept of objects is firmly rooted in the infant's actions directed towards the object, (Piaget 1954) resulting in an increase in interest and activity in both series. This development is apparent first in the social domain, closely followed by the non-social. The Stage 3 behaviors diminish in use, and the more cognitive Stage 4 behavior patterns in both object and "animal" permanence continue throughout the study. In Stage 4, the concept of object permanence is freed from the sphere of activity but is still not fully developed. The infant is unable to conceive of the object as being the same when seen in different contexts (Piaget 1954). For example, although the infant is able to recognize a grape, the grape in mother's hand is perceived as different from the grape in the food bin. Therefore it is not surprising that the developmental patterns of the object- concept and social series are closely related in Stages 2, 3, and 4 since these series represent the gradual acquisition of the notion of social and non-social object permanence, from its total absence in Stage 2 to the context-related form in Stage 4. In Stage 5, the association between the two series weakens possibly because objects are perceived as being independent of the context and are now the target for trial and error, goal-directed actions. The fact that inanimate objects do not respond to the more inventive Stage 5 interactions as do conspecifics could create differences in the levels of actions directed to social and non-social objects.

Piaget and Inhelder (1969:117) stated that in human infant development "cognitive and affective or social development are inseparable and parallel". There is evidence that social relations are critical to the construction of the concept of object permanence in children. Kaye (1982) suggested that cognitive structures in human infants are acquired through social processes, and that knowledge is gained from the infant's and associated adults' joint views of the world. From a very early age, interactions with parents and others provide social cues for the infant (Kaye 1982).

Cheney and Seyfarth (1990), on the other hand, suggest that there is a real distinction between social and non-social cognitive activity in vervets and perhaps other nonhuman primates, and that natural selection has acted to favor some abilities in social contexts that are not transferrable to other situations. They feel that monkeys operate less efficiently when dealing with environmental features and other species than they do in social situations. To emphasize their point of view further, they cite the fact that monkeys often have difficulty learning to solve problems in laboratory tests which they can solve easily in the social domain. An example is the concept of transitivity, which is the ability to understand that if A is larger than B, and B is larger than C, then A is larger than C. Monkeys can learn this concept in the laboratory after a great deal of preparation, whereas they are readily able to grasp the dominance hierarchy in their social group from an early age.

The results of the present study suggest that, at least in the early months of life, the development of cognition in social and non-social domains proceeds in a parallel fashion and that the abilities _are_ transferrable and inter-related. However at the Stage 5 level, when the young cebus monkey was beginning to use inventive intelligence to solve problems, the patterns of development in the respective domains became divergent, with the use of the more cognitively-oriented behavior patterns in the physical world increasing dramatically and the Stage 5 social behaviors diminishing to a very low level. It is possible that as an infant approaches adult capabilities there is less association between the two domains.The increase in manipulatory activity in the young cebus monkey could reflect the added sensory stimulation in the execution of novel and complex actions on environmental objects, and could be expected to be a part of cebus infant development generally. It appeared that as the infant cebus approached the adult level of cognition, the natural propensities of cebus monkeys to investigate and manipulate their physical environment became obvious, overtaking the use of Stage 5 social and locomotor behaviors.

The superior manipulative abilities of cebus monkeys are clearly evident in their foraging strategies. In the wild, they eat an extremely wide variety of plant parts and animal matter which include an number of species of fruit which are only seasonally available, and highly mobile insects (Izawa 1979, Terborgh 1983, Robinson 1984). The monkeys employ an impressive number of strategies to extract choice food items that present difficulties, such as tough palm nuts, termite and wasp nests, and hard to reach fruits (Izawa 1979). Izawa (1979:57) reported that the feeding patterns of *Cebus apella* varies greatly depending on the type of food, suggesting a knowledge of the "nature of plants and the habits of the animals it eats". He described them as intelligent foragers whose feeding behaviors are highly adaptive. Thus it was not surprising to observe the young cebus monkey in the present study using a number of trial and error behavior patterns characteristic of the Stage 5 level of cognitive development in her interactions with objects in the enclosure.

The striking difference between the developmental patterns observed in human and nonhuman primate infants is the absence of repetitive behaviors in terms of object and object-object interactions (secondary and tertiary circular reactions) from the Stage 3 to the Stage 5 levels in the young monkeys. Parker (1977) suggested that repeated interactions between the human infant and physical objects is critical in the development of the ability to judge the properties of environmental agencies, and was likely an important factor in the evolution of tool use. In a social context, circular reactions between the infant and others provides the basis for the development of a self-image, the acquisition of language and other vital social attributes (Parker 1977). There is evidence that cebus monkeys are unusual in this respect and do exhibit a degree of circularity in their behaviors directed towards environmental objects; however, the use of these behavior patterns does not approach the levels seen in human infants.

Antinucci (1989d, 1990) compared the development of object-concept in cebus monkeys, macaque species, and an infant gorilla using the Piagetian model, and found that all infants achieved the Stage 5 level of ability. The young cebus monkeys developed at a slower rate than macaque infants, due to the fact that cebus do not achieve independent locomotion as early in life as the semi-terrestrial macaques. However, once locomotor ability was established in the young cebus monkeys the rate of development speeded up, while in the macaques the developmental rate slowed down. It would be interesting to make the same comparisons between cebus monkeys and macaques in the social domain, given their very different social and physical environments. It is tempting to speculate that some semi-terrestrial species living in large complex social groups such as baboons and Japanese macaques would show much higher levels of Stage 5 social behaviors, given that they are not noted for the same degree of inventive manipulation as cebus monkeys. Chapter 6 will look at the expression of social versus non-social cognition in other species, particularly those living in large complex social groups.

Natale and Antinucci (1989) tested the appearance of representational cognition (Stage 6) in object-concept ability in the cebus monkeys and macaques. They found that the strategies used by these monkeys in their efforts to trace invisible displacements of objects did not indicate the formation and use of mental representations. The gorilla was able to master the same tasks in a manner suggesting the use of a mental reconstruction of the object's movements. Schino et al.(1990) used the same methodology as Natale and Antinucci (1989) to test the development of Stage 6 object-concept in cebus monkeys and crab-eating macaques and found that, although the macaques showed no evidence of using mental images to recover the target object, one adult cebus monkey did appear to possess representational ability. Schino et al.(1990) felt that this result could be an indication of intraspecific variablility in cebus abilities, a possibility that should be explored further. Cheney and Seyfarth (1990) suggested that the social behaviors directed by vervet monkeys do indicate the use of mental representations of their conspecifics and their relationships towards them. However, these researchers argued that vervet cognitive capacities in the social domain are hampered by the fact these monkeys appear to be unable to attribute mental states to others in their social group. The extension of social cognition into Stage 6 will also be explored in Chapter 6.

In summary, rudimentary cognitive behaviors were observed in the young cebus monkey somewhat earlier in the social compared to non-social domains. The patterns of acquisition and use of the concept of object permanence, which is so important in a individual's ability to reason about the world (Lefrancois 1989), were similar in social and non-social areas from Stages 2 through 4, with the more cognitively-oriented stages of behaviors still evident in the infant's behavioral repertoire at the end of the study. This result is an indication that, at this point in the developmental process, there is an association between social and non-social cognition. With the appearance of Stage 5 behaviors, when the use of inventive intelligence became apparent, the infant monkey's propensities for creative manipulation took over from all other activities. It appeared that social cognition developed early and formed an important part of the infant's activities up to the point when the adaptive patterns of adult cebus monkeys, in terms of object manipulation, took precedence in the use of inventive cognition.

Chapter 5. The Development of Social Cognition in Three Nonhuman Primate Species

The Piagetian model used in the longitudinal case study of infant cebus development was applied to short-term studies of infant development in three other nonhuman primate species, the squirrel monkey, the patas monkey, and the ringtailed lemur. This chapter will be divided into three sections which will describe development in the three species separately, paying particular attention to the social domain; and the results of each will be compared with those reported in the previous chapter for the young cebus monkey. These species were chosen with the objective of providing a basis for comparison in terms of several different criteria:

a. Rate of physical maturation - comparing the developmental patterns of precocial and relatively altricial species.

b. Habitat use - comparing developmental patterns between terrestrial and arboreal species.

c. Social Patterns - relating the developmental patterns to the social patterns exhibited by the different species.

The focal animal data in all three studies were recorded by means of a Realistic Miniette tape recorder and subsequently transcribed onto data collection sheets, as in the original case study, using the same basic ethogram (see Appendix 1), with the addition of some species-specific behavior units. The data were sorted and analyzed by computer to produce the following values:

a.The average weekly durations of all behavioral states, which were subsequently adjusted to the average percentage of the total duration per session

b.The average weekly frequencies of all behavioral states and events, presented as the average rates of behavior per session.

c.The average weekly durations and frequencies of behaviors per session observed in varying degrees of proximity to the mother; e.g., on the mother's body, in contact with the mother, closer than 1 m to the mother, and farther than 1 m from the mother.

d.The average weekly durations and frequencies of behaviors broken down into those which were solitary activities and those which were interactions with the respective members of the social group.

e. The average weekly frequencies and durations of the combined critical behaviors (as defined in Appendix 2 for each series in Stages 2 through 5) adjusted to average values per session. As in the previous study, the combined critical behaviors in the social series were those directed to members of the social group other than the mother except where specified. The values used in the analyses were the average weekly frequencies, which are referred to as rates, and the average durations per session of the combined critical behaviors defined in Appendix 2 for each series in Stages 2 through 5.

Section 1: A Comparison of the Development of Social Cognitionin Two Neotropical Primates, *Saimiri* and *Cebus*

The objective of this section is to compare the patterns of cognitive development in two species of New World monkeys, squirrel and cebus monkeys, focusing particularly on the development of social cognition. Although both species are members of the Family Cebidae and are closely related taxonomically and similar in their ecological niche, it is possible that species-typical propensities in the use of the environment play a role in the development of the young.

The Natural History of the Squirrel Monkey (*Saimiri sciureus*)

Squirrel monkeys are among the smallest members of the Family Cebidae of New World monkeys, the males, who are slightly larger than the females, weighing between 700 and

1100 g (Napier and Napier 1968). They live in large multi-male multi-female groups, ranging from 10 to 200 animals depending on the size of the forest (Baldwin 1985, Napier and Napier 1985). They are arboreal animals that move quadrupedally, primarily in the understory of the forest with the occasional trip to the forest floor to forage (Fleagle 1981). Foraging and feeding take up the major portion of their daily activities, as they are constantly on the move searching for insects in the foliage. They are omnivorous, eating fruit, and other vegetable matter; but they prefer insects if available. Since they are unable to crack hard nuts, fruit and tough seed pods, they rely on their speed and agility make up for their lack of strength (Fleagle et al.1981). This agility can be observed in their ability to catch insects on the fly (Fragaszy 1985). Squirrel monkeys can often be found travelling in polyspecific groups with cebus monkeys, scavenging food and taking advantage of the wasteful eating habits of the larger and stronger monkeys (Terborgh 1983).

There is a weak dominance hierarchy in both adult males and females. Adult females are attracted to each other, and their activities regulate group movements. They are the focal point for group activities with all other group members except adult males. and they act to unify the group by this attraction rather than by dominance (Baldwin 1985). Except at mating season, when adult males seek out the females, most of the social actions occur within the same age/sex classes. During mating season, the males build up subcutaneous fat deposits and actively compete for females, who are often agonistic towards their advances. Adult males stay together and rarely interact with infants and young animals (Baldwin 1985, Fragaszy 1985). Squirrel monkeys in the wild are less social than cebus monkeys (Terborgh 1983), grooming each other rarely (Robinson and Janson 1987). However, although they may avoid social contact, group members monitor each other constantly and appear to be strongly motivated to stay within eye contact (Fragaszy 1985).

Squirrel monkeys, like cebus monkeys, have been used extensively in laboratory learning tests, and are able to master most of the tasks set for them; however, they are hampered in those requiring time and concentration by their short attention span and lack of motivation to complete the task (Fragaszy 1985).

Methods

The subject of the study was an infant male squirrel monkey born on October 14, 1989, at the Valley Zoo, Edmonton, Alberta. After two reconnaissance sessions, data collection began on October 16th, in the first week of life, and continued until March 2, 1990, when the young monkey was 20 weeks old. Impending changes involving the addition of two adult males to the zoo colony limited the duration of this study.

A total of 108 observation hours resulted in 54 hours of focal animal data recorded in 10 minute sessions. The activity pattern of the infant dictated the times of day when the data were taken. Although early mornings were usually the most active times, if the infant was sleeping, observation sessions were postponed until he was fully awake.

Physical and Social Environments

The infant male squirrel monkey was born into an ongoing social group consisting of the mother; an adult female the same age as the mother, the father of the infant, who was 13 years old, and a younger adult male. The pattern of interaction between the members of the social group was consistent with that reported for squirrel monkeys in general. The two males and two females spent a great deal of time in like-sex groups, sitting and sleeping in close proximity and interacting rarely with members of the opposite sex. The only exception to this social pattern occurred during two weeks in November when the females were in estrus and became the object of sexual behavior from the two males.

The monkeys were housed in their winter quarters which consisted of a room approximately 2.5 m wide, 4 m deep and 5 m high, with one large observation window in the front. The room was equipped with bars, an imitation tree with a number of branches, a food platform, and a small house set on the bars which afforded the monkeys some privacy from onlookers. Food was provided twice daily at 0730 and 1400 hours; and although the room was cleaned between feedings, some food was available at all times. Water was always available from a spigot on the floor.

Results

A Qualitative Description of Squirrel Monkey Development

New-born squirrel monkeys climb unaided to their mothers' back and generally maintain this position throughout the first weeks of life (Rosenbloom 1968). The dorsal clinging position of the neonate is a dramatic departure from the usual close ventral-ventral attachment seen in other species of monkeys (Rosenblum 1968). Consequently, the mother-infant relationship in squirrel monkeys is quite different from the usual pattern exhibited in other nonhuman primate species, in that the mothers rarely interact with their infants at this early stage. There is no apparent face-to-face visual contact between the mother and the infant; in fact, the mothers often appear to be quite disinterested in the infants on their backs (Rosenblum 1968).

Stage 1

Although the infant spent much of his time clinging to the mother's back in typical squirrel monkey fashion, he occasionally moved to her side or her ventrum. The most striking feature of the infant's early behavior patterns was the number of extended bouts of vigorous, undirected scratching. The neonate did not appear to be able to move his head from side to side but could move on the mother's body in order to look in another direction. Although the other female sniffed the baby and stayed close to the mother, there was a remarkable lack of grooming of the infant or between the females. The infant appeared to be totally unaware of the interest of the other female.

Stage 2

In Stage 2 an infant begins to have more motor control over its actions, and is able to coordinate some rudimentary activities with its world apart from the mother.

The first Stage 2 behavior to appear was in the spatial domain when, in week two, the infant began looking around and moving his head from side to side. By week three, the beginning of Stage 2 in all other areas except locomotion, the infant was becoming extremely active; and exhibited a number of new behavior patterns directed towards the mother, himself, and the environment. The most evident change in activity pattern was the accelerated movement on the mother's body, accompanied by frequent reaching out and touching the substrate. This activity was likely related to his new-found ability to view the surroundings and the fact that he was able to sit upright on the mother's back. Scratching, now directed to a specific body part, still accounted for an inordinate amount of the infant's activity budget. Although he did chew his hand and his mother's fur, the activities in this stage were not nearly as orally-oriented as in the young cebus monkey. The other female continued to try to muzzle the infant, but the mother often pushed her away. Although the infant was unable to grasp the other female, he reached out to her at every opportunity. Stage 2 locomotor actions, which involved crawling on environmental surfaces, appeared much later than other Stage 2 behaviors because the young monkey did not get off his mother's body until the fifth week of life, nor did he lose direct contact with her until week six.

Stage 3

The main advance in Stage 3 sensorimotor-intelligence ability is the ability to coordinate vision and prehension, allowing the infant to interact more easily and efficiently with its environment. The infant, at this stage, is beginning to perceive the permanency of objects, but only to the extent that objects exist when they can be seen and acted upon.

An overlap in the acquisition of Stages 2 and 3 was evidenced in the social series, as the infant began using the behavior patterns of both stages during the third week of life. When the other female was allowed to approach the clinging infant, he tried to feel her with his hands and put his face up close to hers (muzzle). Later in Stage 3, he began to exhibit a more complete range of intentional social behaviors towards her, such as clutching, play face, and social play. The mother began to restrict the infant's access to the nipple at week four, and as Stage 2 progressed she became more vigorous in her attempts at weaning the infant from her nipple and from her body. When the mother's weaning attempts became particularly vicious, the other female would approach the clinging infant and attempt to take him away. In these instances the infant responded by clutching and muzzling the female. He began to eat solid food during this stage; however, any food that he managed to get was from his mother or from the other female. It seemed that the procurement of food represented social rather than nutritional needs.

The beginning of Stage 3 behaviors in the sensorimotor and object-concept series followed at week four while the infant was still clinging loosely to the mother; and he became increasingly more active in his interactions with the environment, leaning on the bars and clutching them with both hands. At this point the infant developed a unique behavior pattern in which he repeatedly reached out, clutched at the air, then brought his hand back to his mouth as if he were catching an insect.

Once the infant left his mother's side at week six and began to locomote independently, his motor skills improved quickly as he began to walk, run, and climb with confidence within a week. The mother began to leave the infant at this point, but he was rarely alone as the other female would immediately approach him and allow him to climb on her back.

Stage 4

At this stage, the first purposeful intelligent behaviors appear as infants begin to be able to coordinate familiar actions to achieve a goal.

The infant reached the stage 4 level in the locomotor and spatial series earlier than in the other areas, as he quickly became confident of his abilities and expanded the speed and scope of his movements. By week eight, he had begun to jump from one surface to another and had established set routes to favorite parts of the enclosure. Perhaps the most striking change in activity pattern during this stage, other than the improvement in locomotor skills, was the time spent attending closely to the activities of the mother and the other female. By week ten, his time was divided between vigorous locomotion, watching the females at close range, and manipulating bits of food beside the other female. The species-typical urine rub (see Ethogram in Appendix 1) had become part of his behavioral repertoire at this point.

The mother became more violent in her efforts to dislodge the infant from her back, action which seemed to trigger more attempts to suckle the mother and the other female. His attempts to suckle the female were always rejected. Although the infant was able to pick up food from the food bin, he still preferred to try to get it from the mother or the female. The infant's social activities during most of this stage were confined to interactions with the other female, as the mother continued to intensify her weaning efforts. However, during the last weeks of Stage 4 the infant became attracted to the younger male, who consistently ignored him. The infant made infrequent attempts to groom the mother early in this stage. The obvious lack of expertise in this area was not surprising, given the fact that the little grooming he received was only from the mother.

Stage 5

The use of inventive intelligence to achieve a goal, often using trial and error behaviors patterns, is the hallmark of this developmental stage.

The young squirrel monkey, now visibly bigger and stronger, continued to be extremely active, moving from place to place; however, no new locomotor patterns were added to his repertoire. The Stage 3 and 4 locomotor skills allowed him to make full use of all areas of the enclosure including the floor, which he had shunned until now. Although the young monkey did not spend a great deal of time interacting with environmental objects, his manipulations of food items had begun to show a rudimentary Stage 5 trial and error quality. He was now experimenting with ways of processing a wider variety of food items with varying degrees of success, and spent time searching for favorite pieces of fruit (grapes). He continued to expand his social horizons spending more time attempting to interact with both males; however, his main social partner was still the other female. The Stage 5 level of social behaviors was mainly confined to tantrums and biting episodes directed at the mother, whose weaning behaviors had become more aggressive.

At the end of the study, the young squirrel monkey was continuing to use Stage 3 and 4 behavior patterns in all areas in a more vigorous and confident manner. Although he spent time manipulating and playing with environmental objects, most of these activities were carried out in a social context, in close proximity with the female and, more rarely, the younger male. The one behavior pattern that remained consistent over the entire duration of the study was the vigorous scratching. There was no evidence that the young monkey was able to solve a problem without the experimentation, indicating that he had not reached the Stage 6 level of cognitive ability.

Quantitative Description of Squirrel Monkey Development

The infant squirrel monkey was more precocious than the cebus monkey, and the respective stages of development were achieved at a much earlier age (Figure 5.1.). The developmental trend common to species that develop rapidly can be seen in the overlap in the appearance of the early stages of development (Gibson 1977). Stage 2 behaviors were observed in the spatial series in the second week after birth, a development which likely reflects the fact that squirrel monkeys cling to their mother's back from birth and are able to view their environment much more easily than those who cling ventrally. Stage 3 behavior patterns followed closely in the third week of life. By Stage 4, the rate of development had slowed somewhat, as this level of achievement did not appear until week seven. This was followed by a seven week lapse before the development of the few Stage 5 behaviors exhibited by the young squirrel monkey (Figure 5.1.).

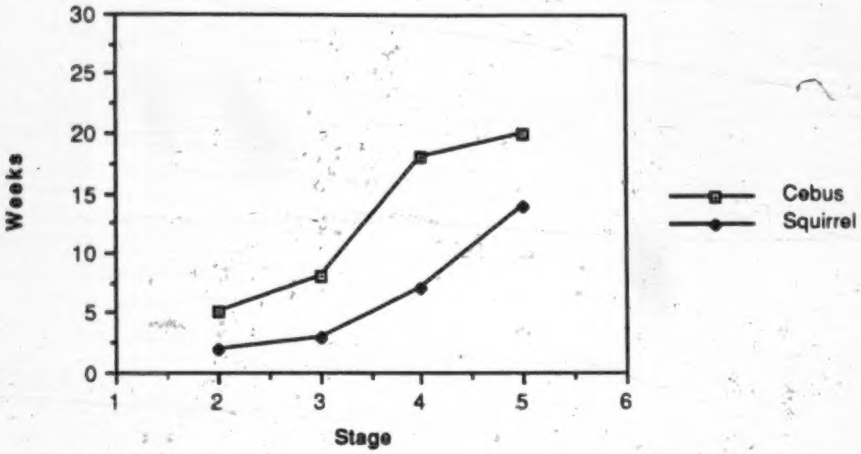


Figure 5.1. Comparison of the weekly acquisition of developmental stages in the cebus and squirrel monkey infants

There was little synchrony in the acquisition of the stages of development in each series until the Stage 5 level was achieved in the sensorimotor, object-concept, and social

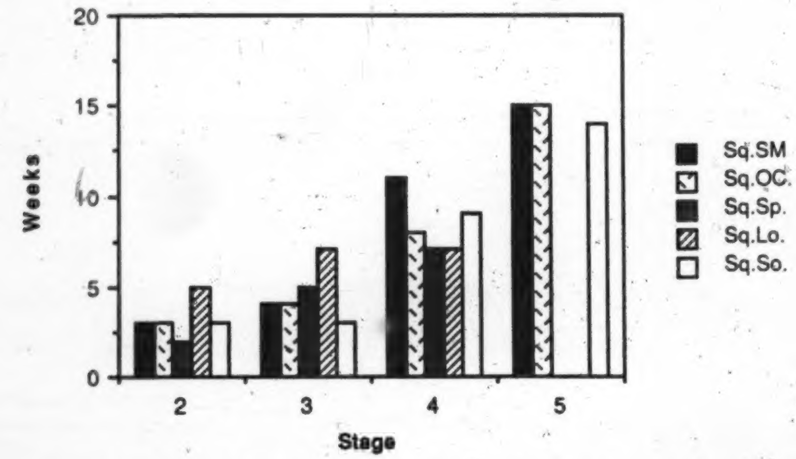


Figure 5.2. The weeks of acquisition of the stages of development of the infant squirrel monkey in the different series

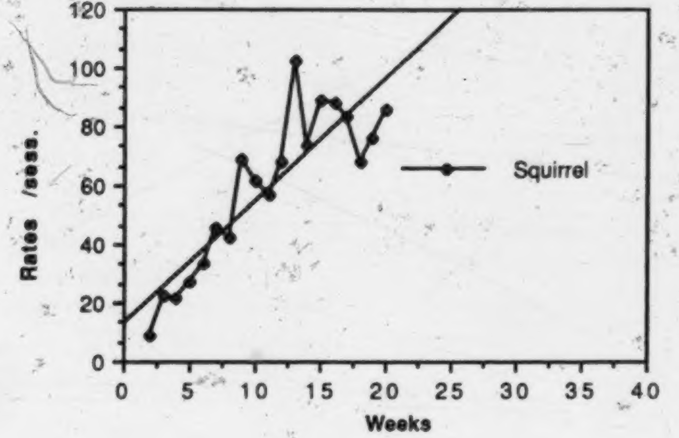


Figure 5.3. The average weekly rates of all behaviors over the 20 week study of squirrel monkey development

series (Figure 5.2.). The patterns of series' development in Stage 3, in particular, was very similar to that of the young cebus monkey, with the appearance of locomotor skills lagging behind those in other areas. This difference can be attributed to the arboreal life-style of both species, in which good hand-eye coordination must be established before an infant can venture out on its own.

In the case of the squirrel monkey, the restrictiveness of the mother was not a factor in the relatively slow appearance of independent locomotion, as the mother began the weaning process at only four weeks of age, even before the infant had left her body.

The increase in the rates of all behaviors proceeded in a relatively constant linear fashion in the early stages of development, peaking at the 14th week when all of the early behavior patterns were well established (Figure 5.3.). During the rest of the study, the rates of behaviors were much more variable, perhaps indicating a tendency for the young monkey to spend more time at specific behaviors, such as locomotion and social interactions. The average rates and durations of the combined critical behaviors in each series viewed separately showed a much greater degree of weekly fluctuation.

Stage 1

Since Stage 1 was of extremely short duration in the young squirrel monkey and there were no socially-directed behaviors during the first two weeks of life, the behaviors were not included in the analysis. The most notable difference between Stage 1 in the squirrel monkey and that of the other species studied was the dorsal clinging position of the infant.

Stage 2 (Figure 5.4.)

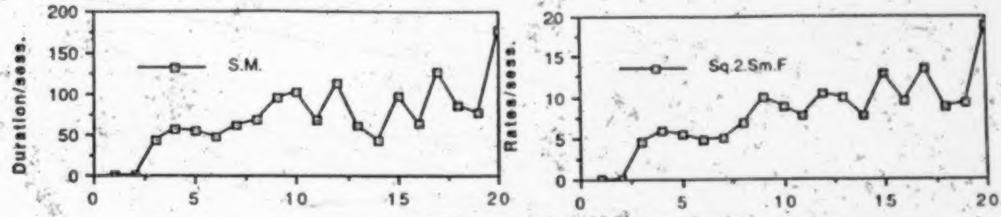
Sensorimotor-intelligence Series - Stage 2 levels of behaviors were particularly evident in this series as the infant began to view the environment and interact vigorously with environmental surfaces at only two weeks of age. The levels of Stage 2 behaviors remained high for the duration of the study, primarily due to the excessive scratching, which was now directed to specific parts of the body.

Object-concept Series - The patterns of emergence and use of Stage 2 object-concept and social behaviors were similar to each other, in that the infant began to interact in a rudimentary way with both physical and social objects at three weeks of age. However, the levels of activity were much higher in the physical domain, as the infant was extremely energetic, moving around on his mother's body and reaching out to feel the substrate.

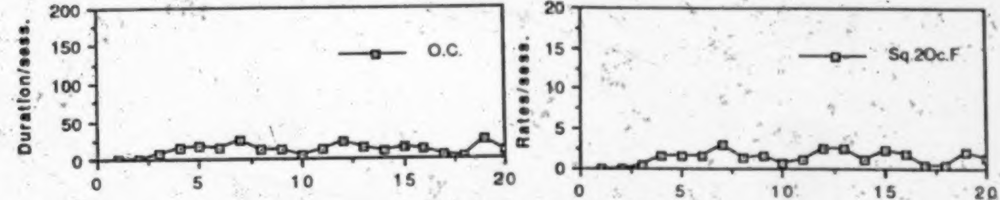
Spatial Series - Stage 2 in the spatial domain began as early as week two when the infant began to move his head from side to side to view his world. The spatial domain also showed a high level of usage throughout the study,reflecting the young squirrel monkey's continuing inclination to look around and attend to everything in his environment.

Locomotor Series - Stage 2 locomotor patterns, did not appear until week five when the infant left his mother's body, well after this level of ability was achieved in the other series. At this point he began to crawl around the bars and branches, keeping close contact with the mother. The movement away from her completely was accomplished at week six, resulting in a dramatic increase in locomotor activities.

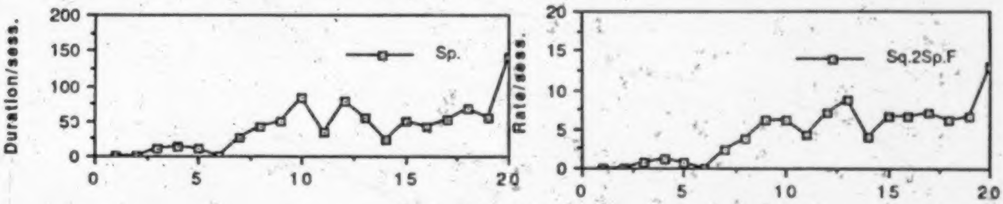
Social Series - Stage 2 and 3 social behaviors appeared simultaneously when the infant was only three weeks old. The young monkey not only reached out and touched the other female when she approached, but actively returned her face-to-face muzzles. This early attention to the physical and social environment could be a function of the infant's position on the mother's back, which would enhance his orientation to things around him. Social interactions were somewhat constrained because of mother's exclusivity in the early weeks, as she rarely allowed the other female access to her infant.



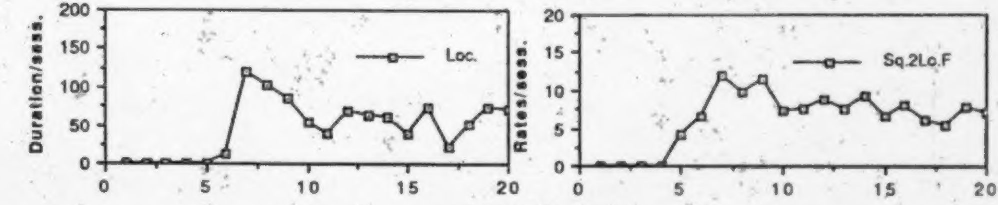
Sensorimotor -Intelligence Series



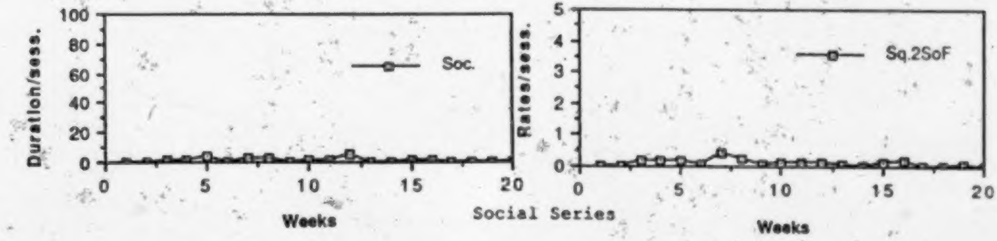
Object-Concept Series



Spatial Series



Locomotor Series



Social Series

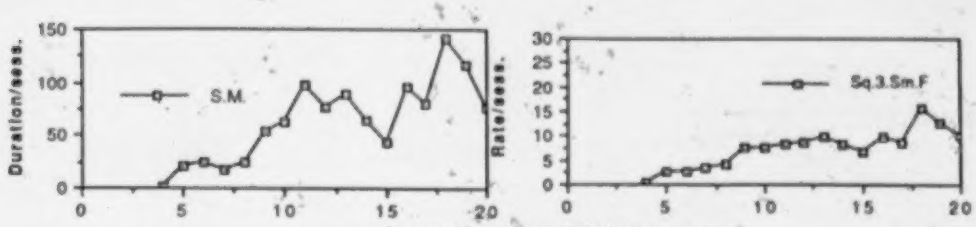
Figure 5.4. The average durations (in seconds) and rates per 10 minute session of the combined Stage 2 critical behaviors of the squirrel monkey

Stage 3 (Figure 5.5.)

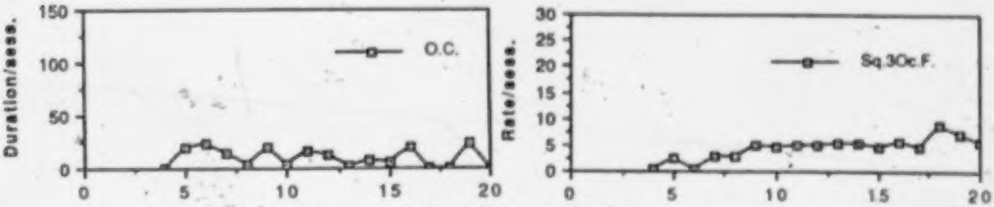
Sensorimotor-intelligence Series- These behaviors continued to be used at high levels throughout the study, reflecting the infant's continuing interest in the environment (clutching and rubbing surfaces). Since eating solid food is incorporated in the sensorimotor series, the peak in the duration of Stage 3 sensorimotor behaviors at about 17 weeks was likely a reflection of the growing infant's improved appetite and increased interest in food.

Object-concept Series - The infant's Stage 3 interactions with the environment were primarily the same behaviors recorded in the sensorimotor-intelligence series, with the addition of solitary play. Actions directed towards environmental objects were not major contributors to the infant's behavioral repertoire at this point.

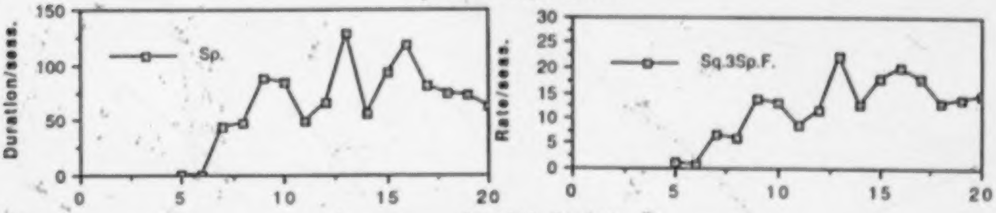
Spatial and Locomotor Series - A number of behavior patterns shown by the young squirrel monkey were included in both of these series. In an arboreal species, the development of spatial cognition goes hand-in-hand with that of Stage 3 locomotor skills. The Stage 3 locomotor behavior patterns emerged after the infant's hand-eye coordination had become well established in social and object-concept behaviors. The sharp increase in the time spent locomoting and the rates of motor actions coincided with the movement of the infant over 1 m away from his mother at week seven. The Stage 3 locomotor patterns continued to be used at a relatively high level throughout the study, a pettern which is not surprising given the fact that these are an arboreal monkey's stock locomotor actions. Stage 4 locomotor behaviors also appeared during the same week; and it seemed that once the infant began to locomote independently, he was able to incorporate more complex activities into his repertoire.



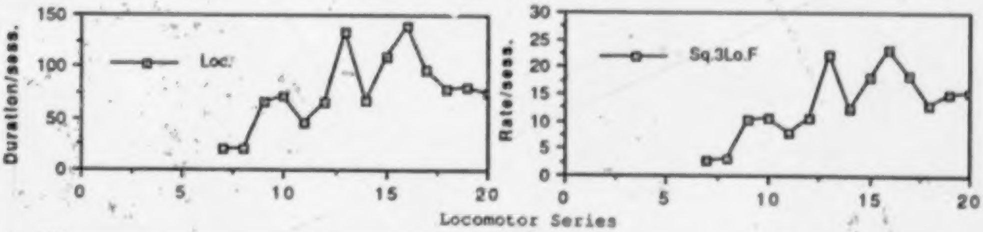
Sensorimotor -Intelligence Series



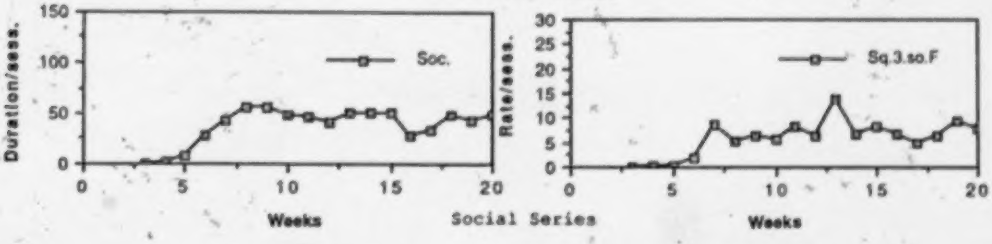
Object-Concept Series



Spatial Series



Locomotor Series



Social Series

Figure 5.5. The average durations (in seconds) and rates per 10 minute session of the combined Stage 3 critical behaviors of the squirrel monkey

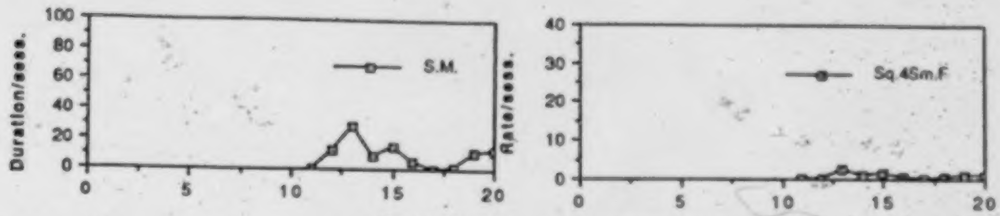
Social Series - Stage 3 social behavior patterns began concurrently with Stage 2 behaviors at week three, a week earlier than in the non-social domains. The infant's capacity to interact with objects in the environment was much more evident in the social domain, as he consistently spent more time in Stage 3 social activities rather than in non-social actions directed to environmental objects such as food. It is important to note that with regard to the acquisition of food, the infant spent more time and effort in trying to take it from the mother and the female than picking it up from the substrate. The increase in socially-directed behaviors after week five were indicative of the ability of the infant to move independently to the female, his only social partner at this point. The Stage 3 level of social behaviors made up a major part of the infant's social repertoire for the remainder of the study.

Stage 4 (Figure 5.6.)

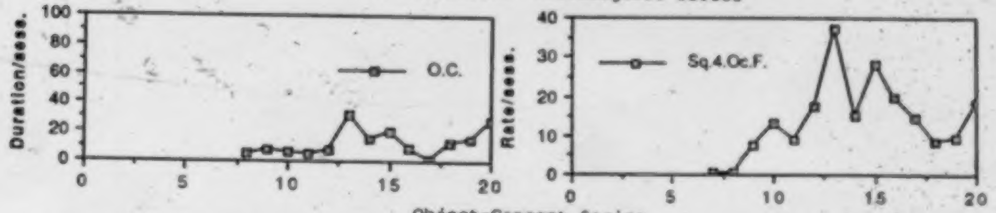
Sensorimotor-intelligence Series - Although the young squirrel monkey began showing some purposeful actions directed towards specific food items typical of Stage 4, the behaviors in this series were mainly confined to those of earlier levels.

Object-concept Series - At this point the rudimentary food processing actions took precedence in his interactions with the environment.

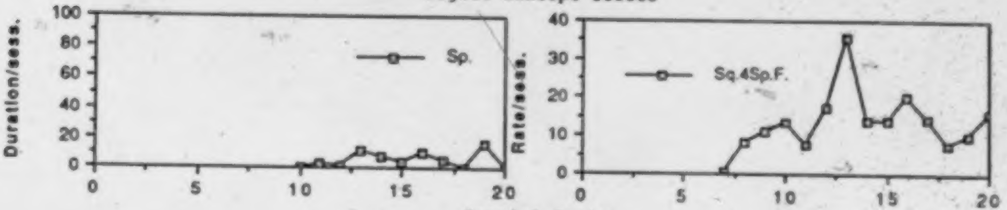
Spatial and Locomotor Series - As in Stage 3, the strong spatial component in all of the infant's locomotor patterns was apparent in the complete overlap of behaviors. The Stage 4 level of locomotor patterns, which began simultaneously with Stage 3 behaviors, were not nearly as well represented in the infant's repertoire as the Stage 3 actions. The main addition to the behavioral repertoire was the ability to jump from one environmental surface to another, an activity which showed up only in the rates of behavior.



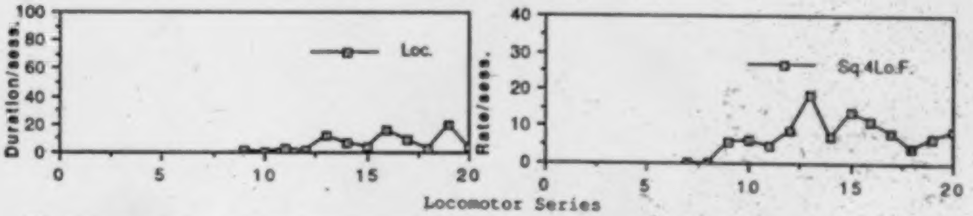
Sensorimotor -Intelligence Series



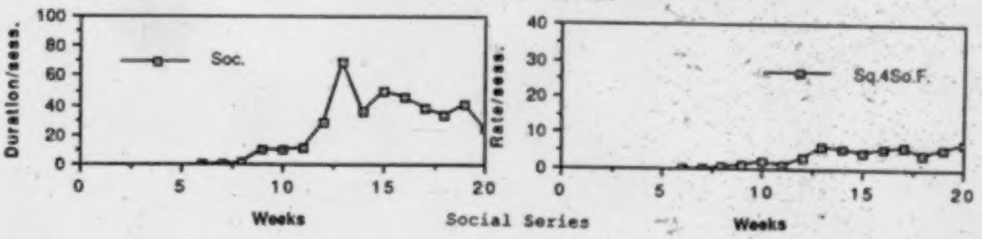
Object-Concept Series



Spatial Series



Locomotor Series



Social Series

Figure 5.6. The average durations (in seconds) and rates per 10 minute session of the combined Stage 4 critical behaviors of the squirrel monkey

Social Series - The average weekly duration of time spent in the more complex Stage 4 object-concept and social behaviors showed a similar pattern, beginning at about the same time (weeks 8-9) and peaking at week 13. However, while the infant was spending more time in social over non-social endeavors, the rates of behaviors were higher in the physically-oriented actions. This apparent contradiction could be explained by the mobile foraging patterns of squirrel monkeys, involving high rates of movements with relatively short durations. Social interactions such as rough and tumble play, on the other hand, would tend to be of longer duration. The almost total absence of grooming in the young squirrel monkey's behavioral repertoire was not surprising given the fact that grooming is rare between adult squirrel monkeys (Robinson and Janson 1987).

Stage 5 (Figure 5.7.)

The few behavior patterns of Stage 5 level of complexity observed in the young squirrel monkey over the 20 week study were recorded when he was 14 and 15 weeks old.

Sensorimotor-intelligence and Object-concept Series - In the sensorimotor and object-concept series the only goal-directed trial and error behavior pattern used was the visual search for specific food items, such as grapes. Since the infant had begun showing a great deal of interest in food, levels of usage of this particular behavior far outweighed those of Stage 5 behavior patterns.

Spatial and Locomotor Series - Although the squirrel monkey infant continued to be active until the end of the study. locomotor repertoire consisted of Stages 2, 3, and 4 behavior patterns.

Social Series - Although the infant used few Stage 5 social behavior patterns, at the end of the study he was a very social animal, spending a relatively high percentage of his average weekly time budget (20%) in the proximity of the

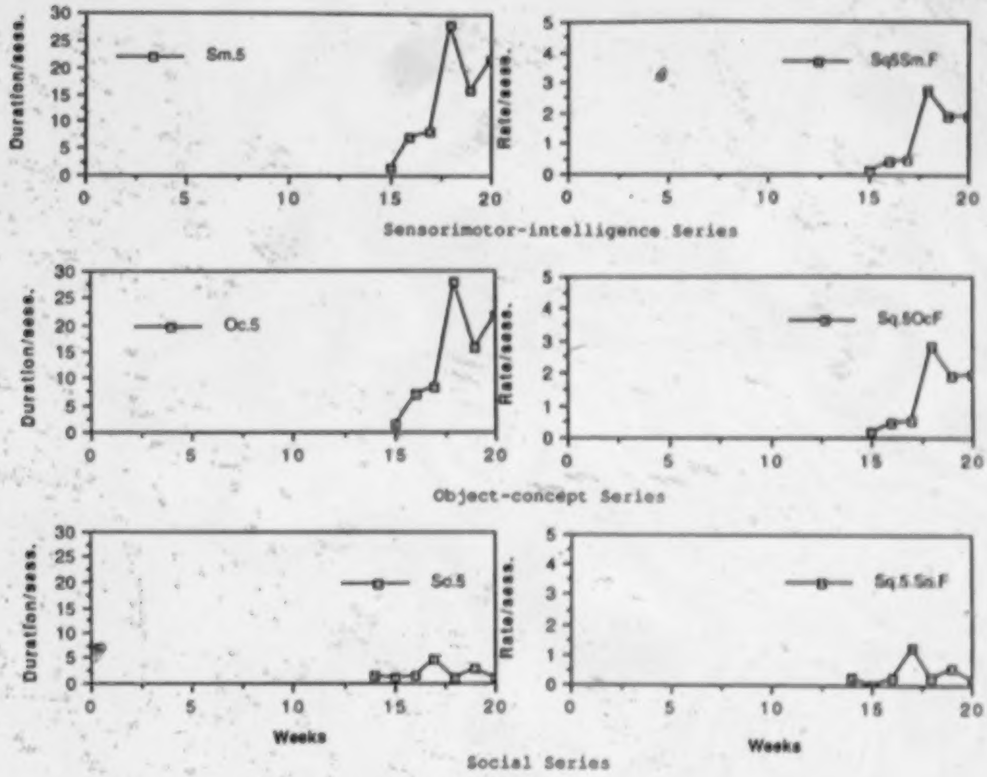


Figure 5.7 The average duration (in seconds) and rates per 10 minute session of the combined Stage 5 critical behaviors of the squirrel monkey

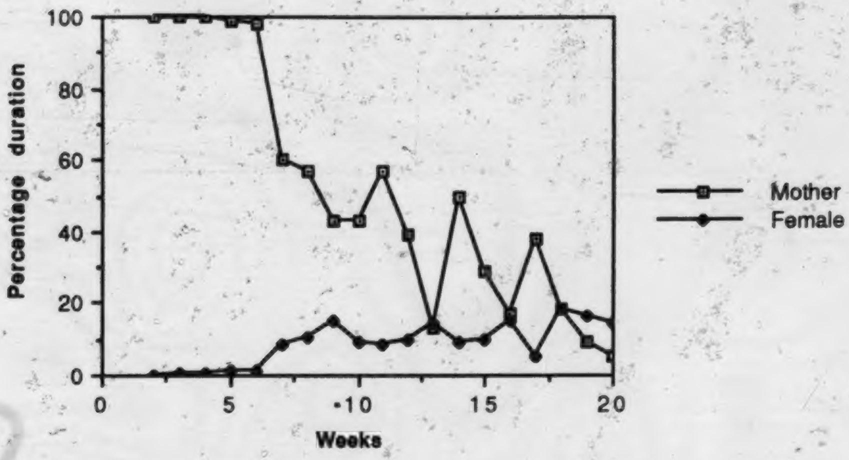


Figure 5.8. The average percentage of time the squirrel monkey spent in proximity to the mother and the other adult female

female, watching her, grabbing for food, and initiating play bouts (Figure 5.8.).

Stage 6

There was never any indication that the young squirrel monkey had achieved the Stage 6 level of cognition indicative of the use of mental representations. At this point he was moving quickly and efficiently around all areas of the enclosure and interacting confidently with the other conspecifics, but was using combinations of familiar actions rather than innovative behavior patterns.

Discussion: A Comparison of Squirrel and Cebus Monkey Development

The cebus and squirrel monkeys are superficially very similar in habitat, diet, activity patterns, and social organization. Both are arboreal monkeys with omnivorous diets, living in the tropical forests of Central and South America in multi-male multi-female societies. Both are able to master the same types of tasks in experimental research and appear to have similar cognitive capacities. This similarity would lead one to expect similar patterns in the development of the infants; however, when one looks more closely at the literature there are obvious differences in their habitat use, foraging patterns, and patterns of interactions within their social group. Fleagle et al.(1981) suggest that the differences in habitat use and foraging strategies are related to differences in body size, the smaller squirrel monkeys foraging restlessly in the lower levels of the canopy while the larger cebus poke, probe, and tear in the middle canopy looking for insects and other food items.

The following is a comparison of the developmental patterns observed in the two case studies, highlighting differences and similarities that are expected to be consistent over infants of both species:

a. Rate of Development - Although the two species belong to the same family of New World monkeys there was a striking difference in the rate of physical maturation. The squirrel monkey infant reached the respective stages of development earlier than the cebus infant. This difference is not surprising given the fact that infant squirrel monkeys are reported to be more precocious than cebus babies (see Figure 5.1.) (Chism 1986). Elias (1977:519) found that "cebus monkeys were less mature at birth than squirrel monkeys in terms of body weight and brain weight in proportion to adult weight"; and that infant squirrel monkeys developed much more rapidly in locomotor, perceptual-motor, and object-permanence capacities.

b. Habitat use - Since both species are highly arboreal, as are all New World species, it was not suprising that the lag in the development of Stage 3 locomotor abilities described for the cebus infant was also evident in the young squirrel monkey. The Stage 3 behaviors, which include quadrupedal walking, running, and climbing, are the basic locomotor patterns used by adults of both species. In both cases, independent locomotion appeared at four to five weeks after the infants had begun to coordinate vision and prehension in relation to physical objects and conspecifics. The appearance of these locomotor abilities coincided with the movement of the infants away from their mother's side when hand-eye coordination was fully established. Once begun, the levels of activity increased rapidly and remained high throughout the rest of the study.

c. Social versus Non-Social Cognitive Development - In both species the patterns of interaction with social and physical environments were very similar in the early developmental stages, beginning at low levels of Stage 2 behaviors which diminished to even lower levels by the end of the study. Again this pattern is consistent with the pattern of development in human infants described by Piaget (1954). The concept of the permanence of objects has not been achieved at this stage, the infant having an "out of sight - out of mind" perception of the world; however with the emergence of the rudimentary notion that objects have a constancy of form at least when physically acting upon them, the early gropings cease. At this point, the infants of both species showed more intercoordination with their physical as compared to their social environments.

The Stage 3 levels of behaviors indicating a beginning in the concept of object permanence and the ability to coordinate vision and prehension were evident earlier in the social domain in the cebus and the squirrel monkey infants, but the patterns of acquisition and use were very similar. In both cases, compared to activities in the other series, interactions with the physical and social environments remained low. The developmental patterns and trends in the object-concept and the social series were very similar in both species in Stages 2 and 3, providing further evidence of the close relationship between the infant's gradual movement from the total absence to the early awakenings of the concept of object-permanence in social and non-social areas at this point in the developmental sequence.

d. The most obvious interspecific contrast in social and non-social object permanence abilities was the manner in which the Stage 4 behaviors were displayed. In the young cebus monkey, the average weekly duration of time spent in goal-directed interactions with the environment rose to relatively high levels compared to the other series, and remained high throughout the study, while the average rates remained relatively low. The pattern of usage of these same behavior patterns were reversed in the squirrel monkey, with a very high rate of behaviors displayed for short periods (Figure 5.9a and b.).

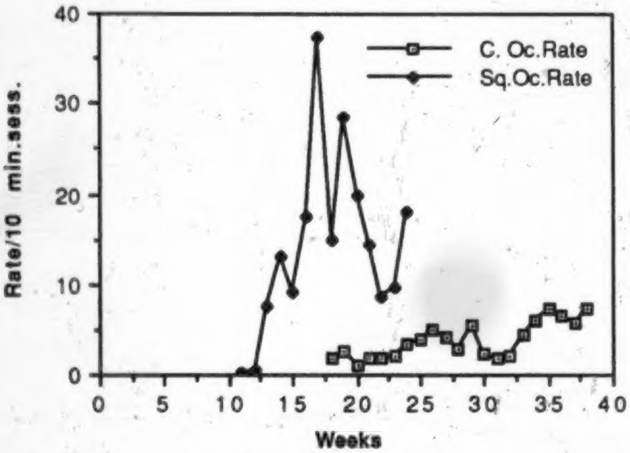


Figure 5.9a. The average rates per 10 minute session of Stage 4 object-concept behaviors of the cebus monkey and the squirrel monkey infants.

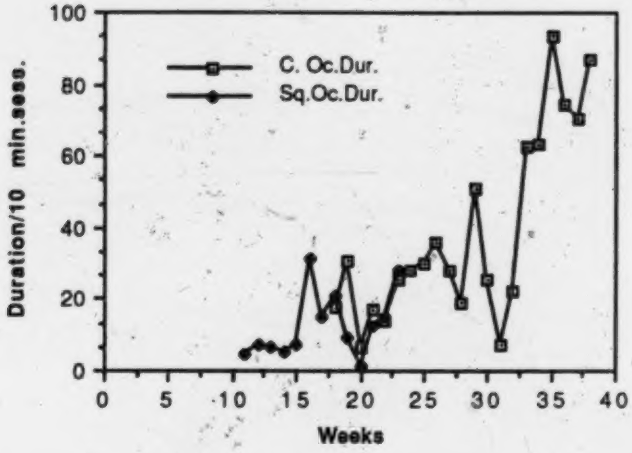


Figure 5.9b. The average durations per 10 minute session of Stage 4 object-concept behaviors of the cebus and squirrel monkey infants.

Cebus monkeys are noted for the time spent in skillful manipulation; and the infant was very active in this area, spending an average of almost 17% of her time in Stage 4 object-concept activities towards the end of the study compared to a peak of 7% of the activity budget in the squirrel monkey infant. The young squirrel monkey, on the other hand, showed the species-typical pattern of peripatetic manipulations of short duration. The cebus activity patterns at this point tended to be more balanced in terms of rates and time spent in interactions with the non-social environment compared to activities in other areas. The cebus infant, once settled into an activity, would continue to pursue it for a relatively extended period of time, while the squirrel monkey's manipulatory actions were fleeting.

e. In cebus monkeys, the time spent in social interactions was markedly less than that spent in non-social manipulations, while the rates in both domains were quite comparable. The pattern was very different in the squirrel monkey, who spent more time in social interactions at a much lower rate of activity.

Although adult squirrel monkeys are not noted for their sociability (Terborgh 1983), Rosenblum (1968) comments on the gregarious nature of the developing infants. Young squirrel monkeys often develop relationships with nulliparous females at about five weeks of life, a relationship that is promoted by the mothers, who actively push the infants into a non-maternal environment (Rosenblum 1968). The infant squirrel monkey followed this pattern, and at the end of the study was spending more time in goal-directed (Stage 4) social activities than in any other area. The fact that the infant did not attempt to groom his mother or the other female was not surprising in that he had rarely been the object of grooming. Instead, from the beginning of Stage 4 in the sixth week of life, he displayed the typical squirrel monkey characteristic of attending carefully to the actions of others (Fragaszy 1985). Although the young cebus monkey was capable of goal-directed social behavior patterns, she was much more active in a non-social sense, spending more of her time acting on the physical environment.

f. The infant squirrel monkey did not attempt to interact with the adult males until late in Stage 4, when the repertoire of adult behaviors was almost complete; and only in the last weeks of the study were these advances reciprocated. This pattern perhaps indicates that the tendency of the males to be intolerant of infants was overcome as the young male squirrel monkey matured, as in squirrel monkey society, like-sex conspecifics tend to associate. The cebus monkey pattern of early social acceptance by the male reflects the tendency for adult male cebus monkeys to be much more tolerant of infant advances.

Summary

Many of the similarities and differences observed when comparing infant cebus and squirrel monkey developmental patterns could be predicted given a knowledge of the rates of physical maturation of the respective species and their adaptations to the physical and social environments. The emergence and use of the basic locomotor patterns in both species lagged behind the behaviors of comparable complexity in all other areas. This is clearly an adaptation to the arboreal life-style of New World monkeys, in which independent locomotion in the trees is related to a well-established ability to coordinate prehension and vision. The young squirrel monkey developed much more rapidly than the cebus infant until the Stage 4 level of cognitive development had been achieved. At this point the abilities of the squirrel monkey did not advance to any great degree, whereas the cebus monkey quickly moved to a number of trial and error Stage 5 manipulations, at least in the non-social domain. Elias (1977) speculated that the longer time spent in perfecting manipulatory and locomotor skills allows cebus monkeys to develop further in these areas. Antinucci (1990) suggested that, since cognitive constructions are developed through interactions with the environment, the longer maturation period would provide a greater opportunity for manipulative skills to enfold. The result would be a richer and more diverse repertoire of behaviors. It is possible that the more rapidly developing squirrel monkeys would have less time to generate elaborate manipulatory constructions.

One of the most obvious behavioral differences between the infants of the two species was the total absence of secondary and tertiary circular reactions shown by the young squirrel monkey in Stages 3 and 5 respectively . This deficit is typical of most species of monkeys, however cebus monkeys are noted for their actions directed towards environmental objects and object-object interactions, many of which are similar to those observed in children. The infant cebus was much more active than the infant squirrel monkey in terms of the manipulation of food items and other objects in the enclosure, some of which showed a degree of circularity.

The young male squirrel monkey was a very socially-oriented individual, spending a major portion of his time watching his mother or interacting with the other female. Even his activities in procuring food were socially-directed; and although towards the end of the study he was searching for food in the bin, he continued to attempt to try to get it from others. Although many of the social behaviors observed remained at the first level of inventive intelligence (Stage 4), they continued to be a major component in the infant's behavioral repertoire. The young cebus monkey, in contrast, spent a much greater portion of her time after reaching Stage 4 in solitary locomotor or manipulatory activities. It appeared that in both species the patterns of development in skillful interactions with the physical and social environments were similar and likely closely related in the early months of life. The patterns began to diverge when the infants began to use trial and error experimentation to achieve a specific goal, indicating the possibility that there is less association or cross-over in social and non-social cognition as young monkeys approach maturity.

It could be hypothesized that, in terms of social cognition, squirrel monkeys who live in much larger and more cohesive social groups than cebus monkeys would be called upon to use their social skills more extensively. Squirrel monkeys are often observed travelling in polyspecific groups with cebus monkeys, and have been described as mildly parasitic on the larger cebus monkeys since they scavenge on the remnants of food left by them (Terborgh 1983). The necessity of keeping on relatively amicable terms with the cebus monkeys would also put an added premium on their ability to be socially adept.

Section 2: The Comparison of the Development of Social Cognition in the Old World Patas Monkey and the New World Cebus Monkey

This section presents a comparison of the cognitive development of an infant patas monkey with that of the young cebus monkey in the demonstration project. These two species of monkeys are not closely related phylogenetically, the cebus being a New World species and the patas belonging to the Family Cercopthecidae of Old World monkeys. In addition, there is a great difference in their habitat use, the cebus monkey being highly arboreal and the patas monkey being noted for its terrestriality. The research will be primarily directed towards an examination of the factors which affect the development of social cognition of the two species; however, development in the non-social dimension will also be an integral part of the discussion.

The Natural History of the Patas Monkey (*Erythrocebus patas*)

Patas monkeys are very distinctive Old World monkeys having adapted to life in extremely hostile areas of Africa (Struhsaker and Gartland 1970). They are the only nonhuman primate species able to exist in the steppe-periphery of the African desert; and are the most terrestrial nonhuman primate species, their long limbs and slim bodies allowing them to move rapidly in open country.

They are omnivorous, surviving on grasses, nuts, fruit and seeds as well as some animal matter in the form of lizards and insects (Struhsaker and Gartland 1970). Patas monkeys live in two types of social groups, heterosexual groups, which range from 5 to 50 animals which include only one adult male and several adult females and their young, and small all-male groups. Although the adult male is twice the size of the female, his role in the heterosexual groups is peripheral, limited to that of a look-out and a diversionary in case of predator attack (Gartland 1975). The male is highly intolerant of other adult males and it is speculated that he is also watching for all-male groups. The females are highly social, forming the core of the social group.They remain in their natal groups for life, whereas the tenure of the adult male may be very short, sometimes lasting for only a few months. Females tend to spend much of their time in nursery groups, and show a high level of allomothering (Chism 1978. Chism et al.1984).

Patas monkeys are small at birth but develop rapidly compared to infants of other Old World monkey species, and are often fully weaned at six months of age. The females are sexually mature at an early age (2.5 yrs.) and reproduce quickly, likely in response to the hostile environment (Chism et al.1984, Chism 1986).

Methods

Data Collection

The subject of this short term study was a male patas monkey infant born on May 3, 1989, in the Calgary Zoological Gardens, Calgary, Alberta. Data collection began on May 11 at the beginning of the second week of life, and continued for six weeks until June 16, 1989. A total of 18 observation hours resulted in nine hours of focal animal data recorded in 10 minute sessions. As in the other studies, no data sessions were begun when the infant was asleep.

Physical and Social Environments

The infant patas monkey was born into a species-typical polygynous social group consisting of one adult male, four adult females including the mother, and one juvenile female.The females in the group were ranked in a definite dominance hierarchy with T-Pau, a four year old, as the alpha female. T-Pring, a four year old female, was the second ranking animal. She was pregnant at the beginning of the study but lost her infant when the young male patas was three weeks old. Mrs. Picton, who ranked next to T-Pring, was one of the mother's principal antagonists. Savak, the mother of the infant, was the most subordinate female; and Sib the juvenile female; born the previous February, was the sister of the infant.

The patas monkeys were housed in The Primate House of the Calgary Zoo in a very spacious indoor enclosure consisting of two adjoining rooms, fronted by windows running along the full width of the facility. This enclosure was connected by a passageway to an equally spacious outdoor facility which was accessible to the monkeys in warm weather. The indoor area was painted in light beige tones with a number of artificial rocks simulating the dry African habitat natural to patas monkeys. The outdoor facility, which was enclosed in wire mesh, resembled the grassland habitat of the patas, having a thick ground cover of grass, a few trees, and some rocky outcrops adjoining the entrance to the indoor area.

The lone adult male in the social group maintained a very peripheral position, spending much of his time at the outer edges of the enclosures watching and occasionally threatening the onlookers. The juvenile female was extremely interested in her young brother, but tended to be rough with him and handled him inappropriately when given an opportunity to take him from the mother. The mother, as the lowest ranking female, was constantly harassed by Mrs. Picton; and was unable to prevent the other females from taking her baby away unless the alpha female was near her. After her miscarriage, T-Pring spent a great deal of time near the mother; and took the baby from her for extended periods, returning him to the mother to be fed. At the end of the six weeks study the infant was still maintaining close proximity to the adult females, but never did come into contact with the adult male.

Results

A Qualitative Description of Patas Monkey Development

Patas monkey infants, like young squirrel monkeys, develop very quickly (Chism 1986,Napier and Napier 1985); and although this was only a six week study, the young male had made a great deal of progress in his manipulatory and locomotor skills. Stage 1 reflexive behaviors exhibited while clinging tightly to the mother's ventrum were replaced by Stage 2 controlled behavior patterns so quickly that they were not included in the qualitative description or the analysis.

Stage 2

The infant, although still spending a great deal of time on the mother's nipple, was extremely active in the second week of life when Stage 2 behaviors patterns began to appear. He was able to sit upright in his mother's lap and move about 15 cms away from her to feel the substrate. At this point, the infant's attempts to crawl farther away were always restrained by the mother. The mother was frequently harassed by Mrs. Picton, and chased around the enclosure with the infant clinging tightly to her ventrum. When T-Pau, the alpha female, was grooming the baby or the mother the other females did not interfere with the mother. The infant was taken away from the mother by T-Pau during the second week of life; and although he resisted somewhat at first, soon settled down with the new caretaker.

Stage 3

The young monkey left contact with his mother and moved over a meter away from her late in the second week of life, reflecting the locomotor and spatial precocity of semi-terrestrial species in general and patas monkeys in particular. Although he was able to grasp environmental objects efficiently from the third week of life on, he did not appear to be interested in picking up food items from the substrate until week five. However, it was interesting to note that the first social gestures addressed to caretaking females were directed towards the acquisition of food. Although the infant was the object of a great deal of attention from T-Pring, who miscarried during his third week of life, all the adult females were allowed to caretake him. The mother was the object of agonism from the main group of females, and tended to remain peripheral to them. By the fourth week of life, the young monkey seemed to be completely comfortable with his allomothers, and began to direct play faces towards them.

Stage 4

This was the last stage achieved by the young patas monkey in the six week study. He was much more confident in his locomotive skills, and was able to jump from one surface to another and use different modes of climbing in the sixth week of life. Stage 4 social skills were evident in the fourth week of life when he began following caretakers after they had left him, rather than running back to his mother. The early appearance of Stage 4 social behaviors was likely a reflection of the high degree of exposure to the other females since his second week of life. Throughout the study, although the young monkey was very active, he was rarely alone, as the females and the mother were very watchful of him. By the end of the study the infant had become extremely playful, particularly with the juvenile female. Although he began attempting to ride dorsally on the juvenile female in the fifth week of life, he was only able to cling tentatively to the backs of his mother and the other females by the end of the study.

Quantitative Description of Patas Monkey Development

Although, generally speaking, infants of New World Monkeys are more altricial than Old World monkeys, the young patas monkey, like the squirrel monkey, developed much more rapidly in every area than the cebus infant. (Figure 5.10.).

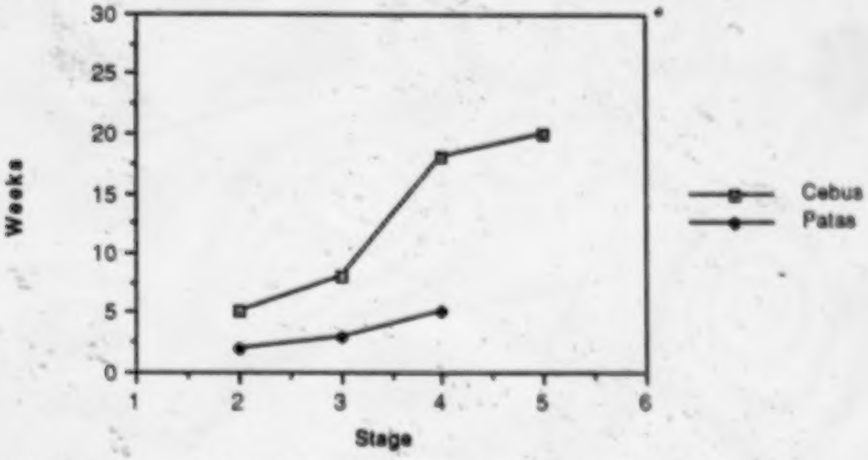


Figure 5.10. Comparison of the weekly acquisition of developmental stages of the cebus and patas monkey infants

Although the accelerated locomotor and spatial development was clearly a function of the semi-terrestrial life style of the species, patas infants in general are very precocial (Chism et al.1984, Chism 1986). Another factor contributing to the early onset of independence from the mother was the high level of caretaking by other females from the second week of life. Due to the subordinate position of the mother, the other females were able to take the infant away from her at will and keep him for relatively long periods of time. This high level of allomothering is consistent with other studies of patas infant development, as Chism (1986) reports frequent infant transfers beginning in the second week of life.

The acquisition of the early stages of development was more synchronous in the young patas monkey than in either the cebus or the squirrel monkey. Stage 2 behaviors were observed in all series in the second week of life; and by week three, the Stage 3 level of ability had been achieved in all but the spatial and locomotor areas. In rapidly developing species, like the patas and squirrel monkeys, there is little space between the achievement of the Stage 2 and 3 skills. The most striking decalage in the development of the infant patas monkey was the early appearance of Stage 4 social behaviors relative to the those in the non-social domain (Figure 5.11.). Soon after the young patas had gained confidence in his locomotor skills he began seeking out the juvenile female (his sister), and attempted to initiate bouts of rough and tumble play. His attention to physical objects in the enclosure was negligable at this point.

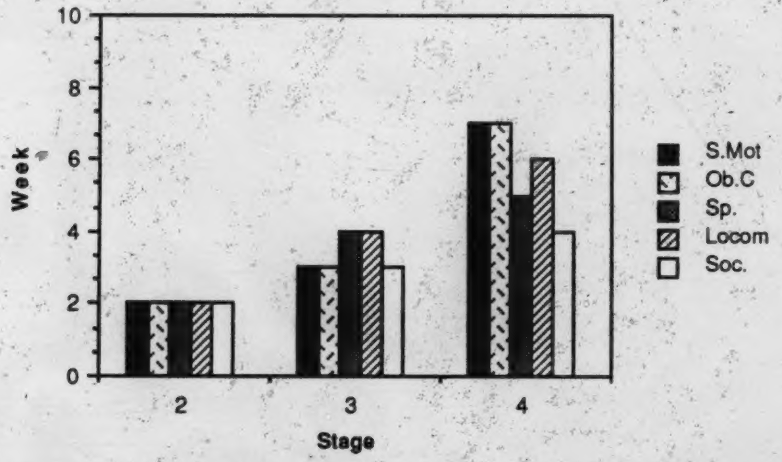


Figure 5.11. The weeks of acquisition of the stages of development in the different series in the infant patas monkey.

Stage 2 (Figure 5.12.)

Early in the second week of life Stage 2 behaviors were observed in all series as the infant began interacting with the non- maternal environment in a rudimentary way.

Sensorimotor Intelligence Series - The infant was extremely alert and attentive to environmental stimuli in the second week of life, and spent a major portion of his waking hours looking from side to side in his mother's lap and fingering the substrate. Since the pattern of usage of Stage 2 behaviors in the spatial series was virtually the same, it was clear that these behavior patterns, which are closely related to the acquisition of spatial knowledge, were major contributors to the time spent in sensorimotor activities. The level of usage of rudimentary intercoordinations with the environment remained high for the rest of the study.

Object-concept series - Although these behavior patterns began in the second week of life, the concept of object-permanence had not yet been established; and the rates and duration of time spent interacting with the environment remained relatively low. These behaviors never did gain any prominence in the infant's behavioral repertoire as he progressed rapidly to the subsequent stages.

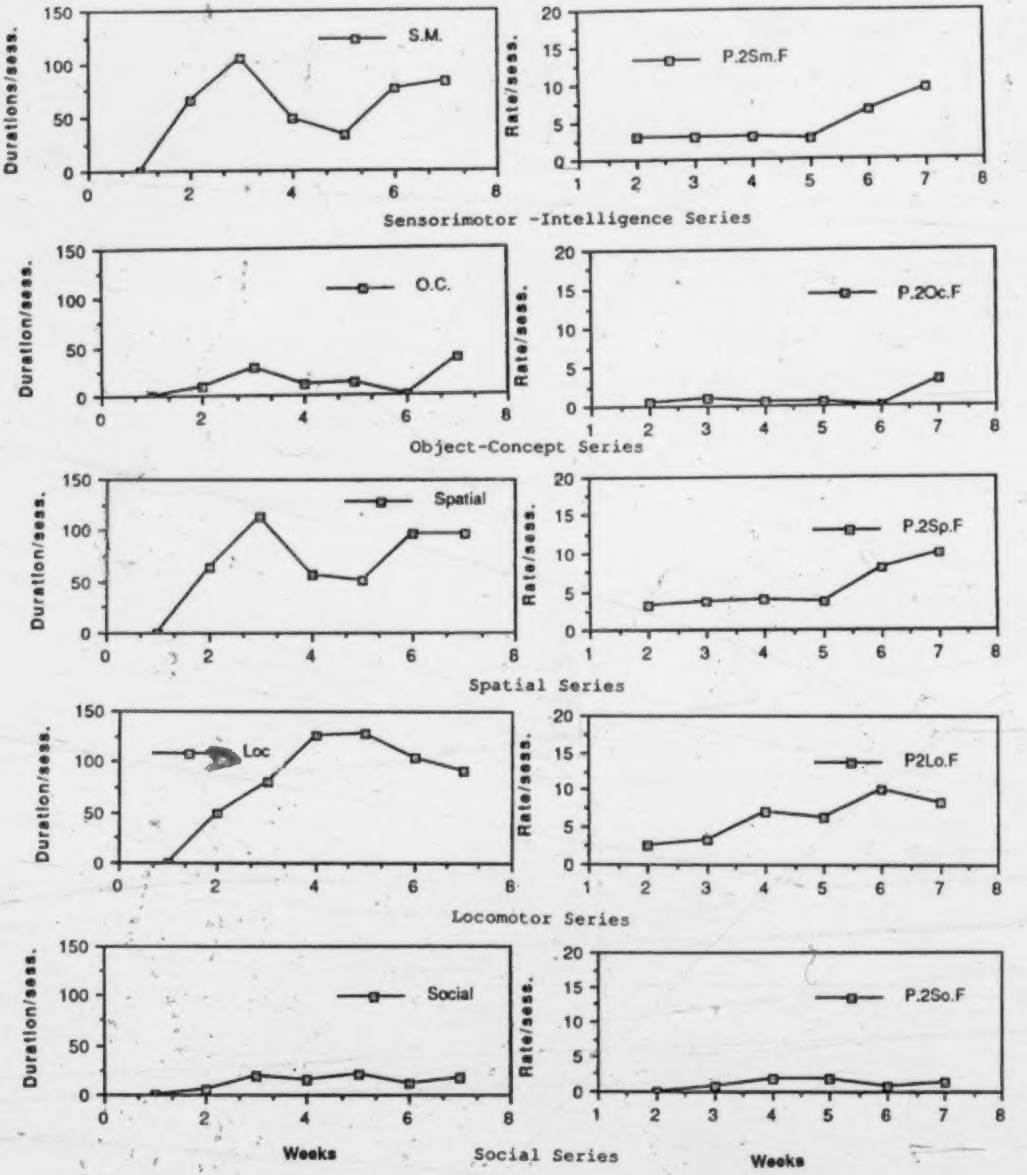
Spatial Series - The early interest in the surroundings indicated by

the amount of time looking around and feeling the substrate was likely an important factor in the degree of spatial precocity shown in the infant's motor activities.

Locomotor Series - The spatial precocity of the infant was also obvious in his usage of Stage 2 locomotor behavior patterns. He was able to move short distances away from his mother; and when he was not sitting looking around, he was crawling around on the floor near her. Although Stage 3 locomotor behavior patterns began at week four, the infant continued to use these early motor actions throughout the study.

Social Series - Although the young patas monkey was exposed to a number of other females in the second week of life and had ample opportunity to interact with them, the level of Stage 2 social muzzles and feels remained very low.

This pattern was likely related to the fact that the concept of the constancy of social objects had not yet been established. These rudimentary social actions were not used



Sensorimotor -Intelligence Series

Object-Concept Series

Spatial Series

Locomotor Series

Social Series

Figure 5.12. The average durations (in seconds) and rates per 10 minute session of the combined Stage 2 critical behaviors of the patas monkey

to any great extent as they were quickly replaced by the more playful socially-directed Stage 3 patterns.

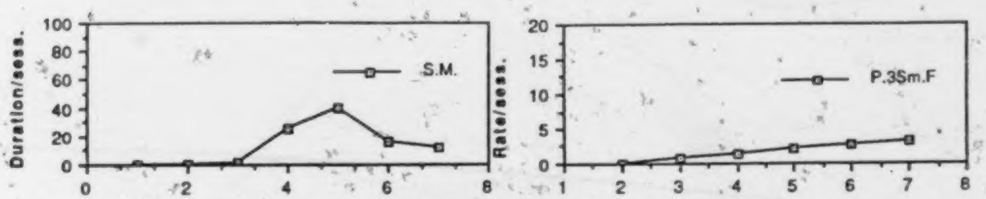
Stage 3 (Figure 5.13.)

Sensorimotor-intelligence Series - The infant was able to grasp environmental objects without groping at week three, but did not show an inclination to do so until week four. The rates of these behaviors, in particular, showed a moderate increase but never did reach a very high level.

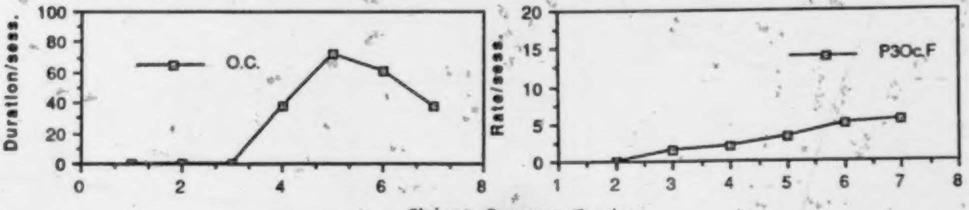
Object-concept Series - The ability to clutch environmental objects efficiently began in week three, and the rates of actions directed towards the environment increased steadily thereafter. The duration of time spent in Stage 3 object-concept behaviors peaked at week five with the onset of solitary play behaviors.

Spatial and Locomotor Series - At this stage, the spatially-directed activities were related almost entirely to locomotion. At week four the infant was able to run, walk, and climb with increasing efficiency, allowing him to investigate the environment. This pattern was particularly evident in the last week of the study when the use of these actions increased dramatically.

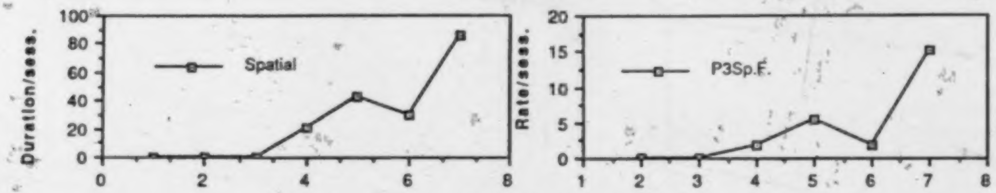
Social Series - The beginning of playful Stage 3 social patterns were observed in week three almost simultaneously with Stage 2 social behaviors, somewhat earlier than this level of behavior in the other series. By week four, the infant had more control over his social activities, as he was able to leave the female caretakers and move back to his mother or another female for a bout of play. The use of Stage 3 socially-directed behaviors levelled off at the end of the study when the Stage 4 social patterns began to take over.



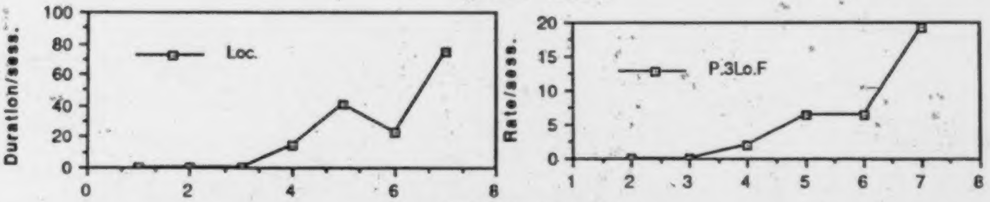
Sensorimotor -Intelligence Series



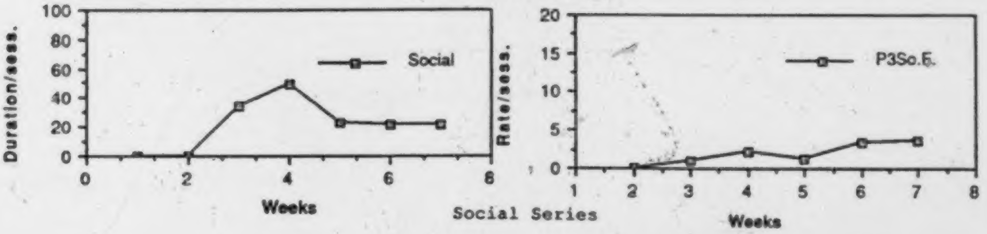
Object-Concept Series



Spatial Series



Locomotor Series



Social Series

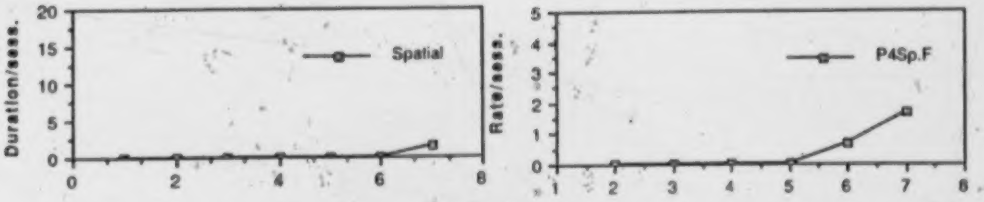
Figure 5.13. The average durations (in seconds) and rates per 10 minute session of the combined Stage 3 critical behaviors of the patas monkey

Stage 4 (Figure 5.14.)

Although the infant was observed using purposeful behaviors in all series by the sixth week of life, the incidence of these actions was so low in the sensorimotor-intelligence and the object-concept series that the rates and durations were not charted.

Spatial and Locomotor Series - The main Stage 4 locomotor action achieved was the ability to jump from one surface to another, a behavior which appeared in the fifth week of life. Since jumping is a behavioral event with no duration, this activity is recorded only in terms of rates. The infant's climbing ability became more efficient and the climbing patterns more varied by the end of the study; but as with the other infant's studied, the main locomotor patterns used were at the stage 3 level.

Social Series - The Stage 4 behaviors began earlier in the social compared to the non-social domain, a development which was likely a function of the young animal's greater mobility and social independence, as he was able to follow specific animals and attempt to initiate play. The sharp increase in the use of Stage 4 social behaviors in the last week of the study paralleled the rise in the use of Stage 3 locomotor activities, indicating the young monkey's increasing degree of independence from his mother.



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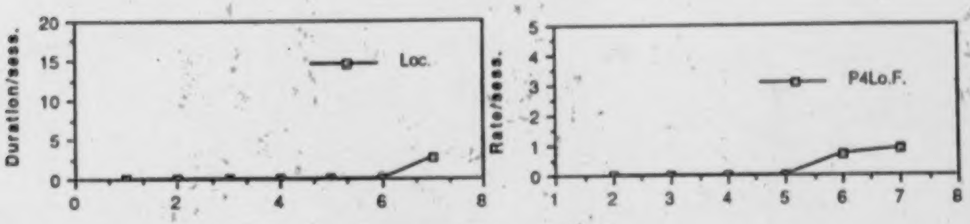
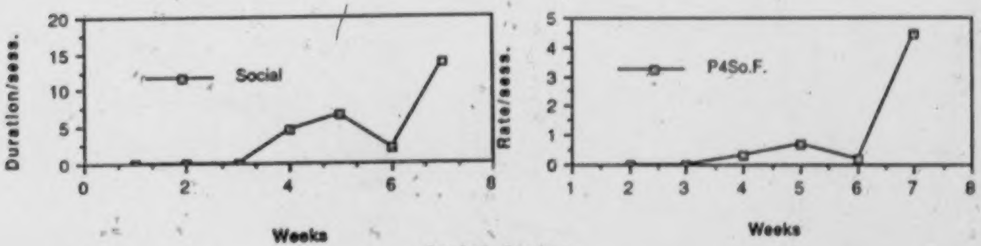


Locomotor Series



Social Series

Figure 5.14. The average durations (in seconds) and rates per 10 minute session of the combined Stage 4 critical behaviors of the patas monkey

Discussion:Comparison of Patas and Cebus Monkey Development

There are clearly observable patterns of development that could be expected to be consistent over all infant patas and cebus monkeys although they represent monkeys from groups split at the Infraorder level, Catarrhini and Platyrrhini respectively. The following are comparisons of these developmental patterns in the infants of the two species:

a. Infant patas monkeys are noted for their precocity compared to other Old World monkey species (Chism 1986), and indeed the second and third stages of development began very early in life (at two and three weeks of age respectively). In some series, the attainment of both stages appeared in the same week of life. Although typically New World monkeys develop more rapidly than Old World species, the infant cebus monkey did not achieve Stages 2 and 3 until the fifth and eighth weeks respectively. The patas infant was capable of tactile and visual exploration of its environment at an early age and showed a rapid development of hand-eye coordination. This advance was evident in both social and non-social domains, as the infant was able to grasp objects relatively efficiently and direct social behaviors fully four weeks before the young cebus monkey was capable of similar behavior patterns. The patas monkey was able to achieve his familiarity with the social and physical environment by virtue of the semi-terrestrial nature of the species, and was able to locomote in safety at an early age. The young cebus, on the other hand, was constrained by the fact that she was unable to leave her mother high above the ground until hand-eye coordination was fully established.

b. The young patas monkey began to direct rudimentary social behaviors towards other group members much earlier than the cebus infant (week two compared to week seven). The social precocity of the young patas monkey was, in part, a function of his early exposure to the other females. Although the subordinate position of the mother facilitated the infant transfers, Chism (1986) reports this phenomenon in all eight of her infant subjects by the second week of life. Allomothering is not a prominent behavioral phenomenon in cebus monkey society although; the other cebus females were interested in the infant from birth, their social attentions were confined to grooming and muzzling.

c. The most striking difference in the rates of development of the patas monkey compared to that of the cebus monkey was the early onset of independent locomotion in the patas infant. This difference was not surprising, given the differences in habitat use. Clearly, the young cebus monkey, being arboreal, would need to be fully competent in hand-eye coordination before attempting to leave her mothers' side and locomote on branches or bars. In the young patas monkey the movement away from the mother could be accomplished in safety without the ability to coordinate vision and prehension.

d. Although the timing of the appearance of the stages differed greatly, the patterns of Stage 2 and Stage 3 object-concept and social development in the patas and cebus infants were very similar, with slightly greater durations of time spent in physical as opposed to social object interactions. In both species the rates and durations of time spent in Stage 2 levels of these behaviors were low relative to the other series. The levels of Stage 3 behavior patterns showed the same imperfect, action-oriented degree of understanding social and non-social object permanence in both the cebus and patas infants.

The similarity in the pattern of acquisition and use of object-concept and social activities in both infants could only be noted for Stages 2 and 3. The young patas monkey had begun to show the Stage 4 level of capability in the social domain in his fourth week of life; and by the end of the study at week seven, these behaviors were becoming an important part of his repertoire. In contrast, the purposeful manipulation of food items and other environmental objects did not appear until the last week of the study and consequently were used minimally at this point. The rapid development of social skills in patas monkeys is not surprising given the fact that that they reach sexual and social maturity at such an early age (Chism 1986). Again it appeared that the relationship between the gradual appearance in the early development of social and physical object permanence was obvious in the patterns of development at least in Stages 2 and 3. The difference between the behavior patterns of the two infants was particularly obvious once they had acquired the ability to use familiar patterns to achieve a goal. The young patas monkey was an extremely social animal from the beginning of Stage 4, frequently approaching the other females in order to play, while the cebus monkey was drawn towards investigating or pulling apart various items in the enclosure.

e. There was a total lack of contact with the adult male in the patas group, behavior which was very different from the cebus adult male's evident interest in the cebus infant. This could be predicted by viewing the respective species-specific social patterns. The patas male is always peripheral to the group, interacting rarely with the females and infants, unlike the cebus males who are often central to the social group and very tolerant towards infants (Fleagle 1981, Chism 1986).

Summary

The comparison between the development of social cognition in the young patas and cebus monkey infants can best be summarized in three ways, in terms of habitat use, the degree of allomothering, and the relative speed of development.

1. Habitat Use - Comparing the development of the semi-terrestrial patas infant with that of the arboreal cebus monkey infant.

Since the patas monkey is the most terrestrial of any nonhuman primate, spending the majority of its time on the ground, and the cebus monkey is a highly arboreal New World species the contrast between these species in terms of locomotor development was especially striking. The young patas monkey was able to move from his mother using Stage 2 motor actions (crawling) in the second week of life, and had progressed to the Stage 3 locomotor abilities (walking and running) a few weeks later. These abilities appeared well before similar behavior patterns were apparent in the arboreal infant, who required a well-developed coordination between vision and prehension before venturing out alone. The early onset of independent locomotion gave the young patas monkey the advantage in a social sense as well, because he was able to choose and approach perspective social partners rather than relying on them to approach him. This social precocity was especially evident in the onset of the more cognitive Stage 4 social behaviors 14 weeks before the cebus infant was at a similar level of sociability.

The terrestrial nature of the patas monkey could also be said to to contribute to the safety and ease with which the females are able to take the infant away from its mother at a very early age.

2. The Degree of Allomothering - Comparing the relationship between the developmental pattern and the degree of allomothering in the two primate species.

The early exposure to other females was also clearly a factor in the social precocity of the patas infant. The patas infant's extension of social bonds from the mother to other females in the first few weeks of life could be seen as a consequence of extensive allomothering. As Chism (1986:49) suggested " The pattern of rapid social and sexual development can be viewed as a response to a highly seasonal savannah environment in which there is a premium on ability to achieve nutritional, locomotor and social self-sufficiency as quickly as possible". In cebus monkey society the females in the social group are interested in infants and pay close attention to them, but do not take them away from their mothers until the infants are able to make the transfer themselves.

3. Rate of Development - Comparing the development of the precocial patas infant with that of the more slowly maturing cebus infant.

The rates of development in the patas monkey infant was considerably faster in all areas than that of the cebus infant (see Figure 5.10.). It is interesting to note that the developmental pattern of the cebus infant, like that of human infants, shows a sizeable time lapse between the acquisition of Stage 3 and 4 behavior patterns (Antinucci 1989) which was not observable in the young patas monkey.

The patas monkey was more socially adept at a much earlier age than the young cebus monkey. This social precocity appeared to be a function of related factors, the semi-terrestrial ecological niche and, the degree of allomothering as well as the pattern of rapid development in patas monkeys. The patas infant was able to make use of the early onset of independent locomotion to extend his social contacts with the other females who had been his caretakers from the second week of life. In terms of intercoordinations with physical agencies, although the infant had acquired the necessary skills at a much earlier age than the cebus monkey, at the end of the study the young patas monkey was much less active in this area.

When the infants of the two species reached Stage 3 level of cognitive organization, the most obvious behavioral difference was the total lack of secondary circular reactions directed by the patas infant towards objects in the enclosure. Human infants at this stage spend a great deal of time and energy acting repeatedly on anything within their reach that produces an interesting effect. Although the young cebus monkey did not achieve the degree of circularity seen in children, she could be observed banging and rubbing food items on the bars. The young patas monkey was very active in terms of Stage 3 and 4 social behavior patterns; however, there was also a marked absence of the circularity evident in a human infant's social interactions.

Although cebus and patas monkeys belong to different infraorders within the Order Primates, contextual factors in the physical and social environments of the two infants, their specific types of adaptive patterns, and the speed with which they mature could have contributed to the interspecific differences in the development and use of social cognition. Although generally speaking, New World monkeys are more precocial than Old World species, the rapidly maturing patas infant was the exception to the rule. This development is seen as a response to the pressures of life in a harsh, unpredictable, highly seasonal environment which would put a premium on the ability to grow up quickly physically and socially (Chism 1981, Chism et al.1984). Cebus and squirrel monkeys live in the tropical forests of Central and South America where resources, although not always abundant, are not as unpredictable as in the arid areas of Sub-Saharan Africa and the forces selecting for early maturation may not be as great. It is possible that in the case of the cebus monkey, with the longer period of maturation and time spent practising manual operations, selection was directed towards extensive and elaborate manipulative abilities allowing greater access to embedded food in the tropical forest environment.

Section 3: A Comparison of the Development of Social Cognitionin a Prosimian Species and a New World Monkey

This section deals with the comparison of the development of social cognition in a prosimian and a New World monkey species. Ringtailed lemurs (*Lemur catta*) are particularly well-suited to a study of social cognition, in that they live in relatively large groups and their social behavior patterns rival those of most anthropoid species (Taylor and Swanson 1985). The comparison with the social development of an infant cebus monkey should prove particularly interesting given the clearly observable differences in the behavior patterns of the adults in both species.

The Natural History of Ringtailed Lemurs (*Lemur catta*)

Ringtailed lemurs are diurnal prosimians found only on the island of Madagascar. They live in large cohesive multi-male multi-female groups ranging from 10 to 24 animals (Richard 1987). They are predominantly semi-terrestrial primates, travelling on the ground and foraging for fruit, flowers, and seeds in all levels of the trees (Richard 1985). They are cat sized animals whose most striking feature is the long plumed black and white striped tail which is used for recognition and as a means for dispersing pheromones. Their wet noses and scent glands are physical adaptations attesting to their reliance on the sense of smell (Tattersall 1982). As a consequence of the strepsirhine nasal structure, the upper lip is immobile, limiting the range of facial expressions. *Lemur catta* have the typical prosimian dental comb formed by the lower incisors and canines which is used extensively for grooming and foraging (Napier and Napier 1985).

Infant ringtailed lemurs are very precocial, and are able to move around actively on their mother's body within a few days of birth (Klopfer and Boskoff 1979). The core of the social group centres around the females, who are extremely permissive with their infants, allowing other females to groom them and carry them around. The females often exhibit a well-defined dominance hierarchy; and are generally dominant over the males in the group, particularly in regard to access to preferred foods (Budnitz and Danias 1975, Gould 1990). Studies indicate that female *Lemur catta* spend their entire lives in their natal troop, while the males show a widespread tendency to transfer between groups (Jolly 1966, Budnitz and Danias 1975).

Methods

Data Collection and Analysis

The subjects of this study were three infant *Lemur catta* born in the Calgary Zoological Gardens in Calgary, Alberta. The two male infants were born on February 26 and March 9, 1989, and the sole female on March 2, 1989. The major difference between this study and the previously discussed research was that the data collection did not begin until April 3, 1989 when the infants were four, five and six weeks old, well past the early stages of development. The study continued for 11 weeks, until June 16, 1989, at which point the oldest lemur was 16 weeks old, the age at which *L. catta* infants are reportedly approaching independence from their mothers (Richard 1987, Gould 1990). Time constraints plus the fact that *L.catta* young are reported to be relatively mature at 16 weeks of age dictated the length of this study.

A total of 95 hours of observation, including reconnaissance sessions, resulted in 66 hours of focal animal data recorded by myself and a research assistant in 10 minute sessions. At the beginning of data collection it was clear that the the infants had established relatively stable daily activity patterns consisting of bouts of vigorous activity interspersed with periods of suckling and sleep. Observation sessions were conducted at the beginning of active times, and concluded when the animals became drowsy. Data were collected when the zoo was closed and after it was open to the public; however, it was clear that the animals were completely habituated to the presence of onlookers.

Before the data collection was begun, my research assistant and I reviewed a video tape of *Lemur catta* adults and infants from the Duke Primate Center and a video tape of my initial case study of the cebus infant in order to test the interobserver concurrence on the critical behaviors to be recorded. The behaviors were distinct enough to allow us to achieve an average of 97% concurrence for 10 minute sessions. Further interobserver reliability tests were conducted on the subject animals prior to data collection and subsequently during the study, with the achievement of an average consistency rate of 94.3%.

Since the infants ranged from four to six weeks of age at the beginning of the study, the results were pooled in terms of the age of the infants in weeks. This practice allowed me to cover the development of the *L.catta* infants from four to sixteen weeks of age in the eleven week study. The values for four week-old lemurs consisted of data taken on Eric (the youngest) only, the values for five week-olds were averages for Eric and Yolanda, the values for six to fourteen week-olds were averages from all three infants, the values for fifteen week-olds were averages for Yolanda and Amos, and the values for sixteen week-olds were from data taken on Amos (the oldest).

Physical and Social Environments

The three *L. catta* infants were born into an ongoing social group consisting of the following animals:

Ciccada- 12 year old female. The mother of Amos, the oldest infant.

Cicely- 8 year old female. The mother of Yolanda, the middle infant.

Yvette- 2 year old female. The mother of Eric, the youngest infant.

Anneka- female 1 year 9 mo. The mother of a stillborn infant.

Shane- Adult male. The father of all the infants.

The adult male was clearly subordinate to all of the females, a pattern which was consistent with the species-typical dominance pattern for *L. catta* (Gould 1990). This dominance was most obvious at feeding time, when the females would not allow Shane access to the food until they and their infants were satisfied. The female dominance hierarchy was well-established, with the two dominant females, Cicely and Yvette, and their infants forming one small social group, leaving Ciccada and her infant, Anneka, and Shane to groom each other and sleep together.

The animals were housed in the Primate House at the Calgary Zoo in an indoor enclosure measuring approximately 4 m wide by 3.5 m deep by 3 m high. The viewing area covered the entire width of the enclosure, allowing an unrestricted view of the animals. The lemurs were able to exercise their full range of locomotor activities on numerous artificial stumps, trees, and branches. The floor was painted a mottled green simulating the leaf litter which would normally be found on the forest floor. The animals were fed fruit and vegetables once daily; however, a tray of high-protein pellets was always available to them.

Results

A Qualitative Description of *Lemur catta* Development

At the beginning of the observations, when the infants were four, five, and six weeks old respectively, they were all riding dorsally on their mothers, and all but the youngest were able to climb the trees. It was clear from their ability to pick up pieces of food with ease that they had achieved the ability to coordinate vision and prehension, which is one of the major accomplishments of the Stage 3 level of sensorimotor-intelligence development. Their competence in the trees indicated that the two oldest infants had reached the Stage 4 level in the locomotor series.

Stage 3

In the first week of the study all of the infants were off their mothers and able to locomote on their own, although Eric (the youngest) did not venture far from his mother until the second week. At this point, when he was five weeks of age, although he was not as sure-footed as the others, he ventured over 1 m away from his mother. The other infants were extremely active, running and climbing; and were even able to complete short jumps from one surface to another. The oldest infant, Amos, was the only one observed grooming his mother and attempting to self-groom his tail.

The most striking behavioral phenomenon in the lemur social group at this stage was the particularly high level of allomothering. The older infants were able to jump on any of the females at will, and tended to remain with their caretakers for extended periods. It was not unusual for a female to have one infant on her back and another in her lap.

Stage 4

All of the infants were extremely active from the second week of the study (weeks five, six, and seven of life), as they were able to jump from one surface to another with increasing efficiency. It appeared that the beginning of the fifth week of life was a landmark for the youngest infant, as he began to catch up with the others in terms of locomotor abilities. Locomotor and rough and tumble play from this week until the end of the study continued to be the main preoccupation for the infants. They spent almost all of their waking hours whirling around the enclosure, leaping, chasing, tail-pulling and wrestling with each other. The remainder of their time was spent in bouts of self-grooming or allogrooming with the mothers and other females. Very little time was spent in manipulating bits of food or other environmental objects such as twigs. Although the infants always returned to their mothers to suckle and sleep, from the third week of the study on they spent very little of their active times near them (Figure 5.15.)

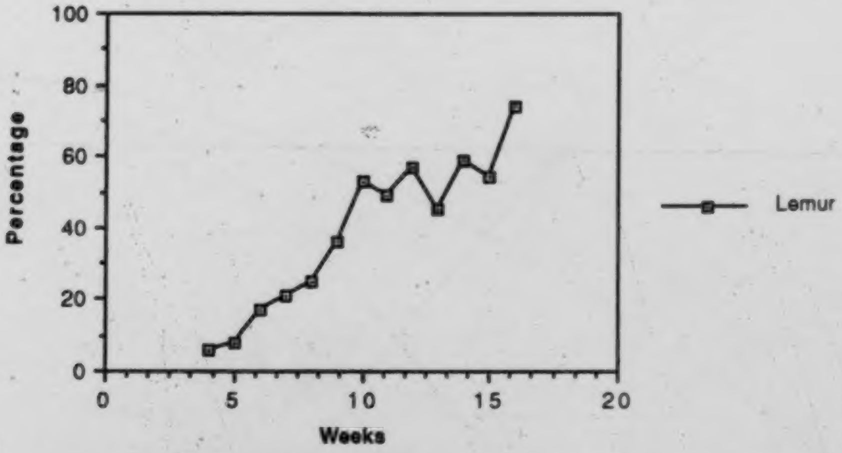


Figure 5.15. The average percentage of time per session spent over 1 meter from the mother.

As the weeks progressed, the infants became more confident of their locomotor abilities; and developed new variations of climbing, hanging and swinging which they incorporated into their patterns of locomotor play. By the end of the study they had extended their jumping ability to cover distances in excess of 2 meters. Although their locomotor prowess was spectacular and exciting to watch, the behavior patterns were combinations of Stage 3 and 4 level activities.

Stage 5

The young lemurs only reached trial and error Stage 5 behavior patterns in the social series. By the eighth week of the study, when the infants were 11, 12, and 13 weeks of age, they were approaching adult size and were beginning to be rejected by their mothers. Shortly after this period the infants began showing aggressive behaviors towards their mothers and the other infants. The fights, consisting of bites, pushes, and cuffs, were quite distinct from the bouts of play wrestling. The periods of grooming and play increased in duration as the study progressed, and it appeared that the infantile sporadic types of behavior were being replaced by more stable adult patterns. At the end of the study, social interactions (grooming and fighting) and socially-directed locomotor activities (chasing and wrestling) made up the major portion of the young animal's activity patterns.

Quantitative Description of *Lemur catta* Development

Infant lemurs typically develop very rapidly, and this pattern appeared to be the case in the present study. Observations did not begin until the youngest infant was four weeks old, and it was clear from the level of the critical behaviors exhibited by him that he was fully in Stage 3 in all of the series. The other infants, at five and six weeks of age, were beginning to exhibit goal-directed Stage 4 behaviors.

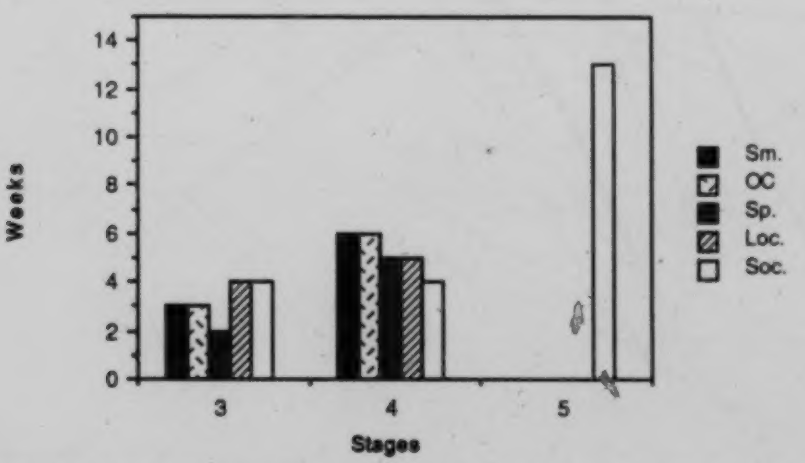


Figure 5.16. The weeks of acquisition of the stages of development of the infant *L.catta* in the different series

Extrapolating from the results of a developmental study conducted on free-ranging *L.catta* (Gould 1989), it was inferred that the infants in the present study would have been riding dorsally on their mothers at week two, and were capable of picking up food and other environmental objects during the third week of life. Therefore it was assumed that Stage 3 in the spatial series began at week two, and in the sensorimotor-intelligence and object-concept series at week three

The infant lemurs did not achieve synchrony in the appearance of the five series in any of the developmental stages (Figure 5.16.); and, as is often the case in rapidly maturing species, there was an overlap in some areas of development (Gibson 1977). This situation could be observed in the social series, with the appearance of Stage 3 and Stage 4 behavior patterns during the fourth week of life. Subsequently there was a lengthy delay of nine weeks before the appearance of the Stage 5 level of capability, which took place only in the social series.

Stage 2 (Figure 5.17.)

Although all of the infants had advanced well beyond the appearance of Stage 2 behavior patterns, it was interesting to note the continued use of these activities.

Sensorimotor-intelligence series - The high levels of these behaviors shown by the infants, especially after they were 10 weeks old were due mainly to their constant attention to their physical and social surroundings. When they were not actively locomoting around the enclosure, they were attending to it visually.

Object-concept series - Unlike the other nonhuman primate infants studied, the young lemurs spent relatively little time licking or feeling the substrate or environmental objects.

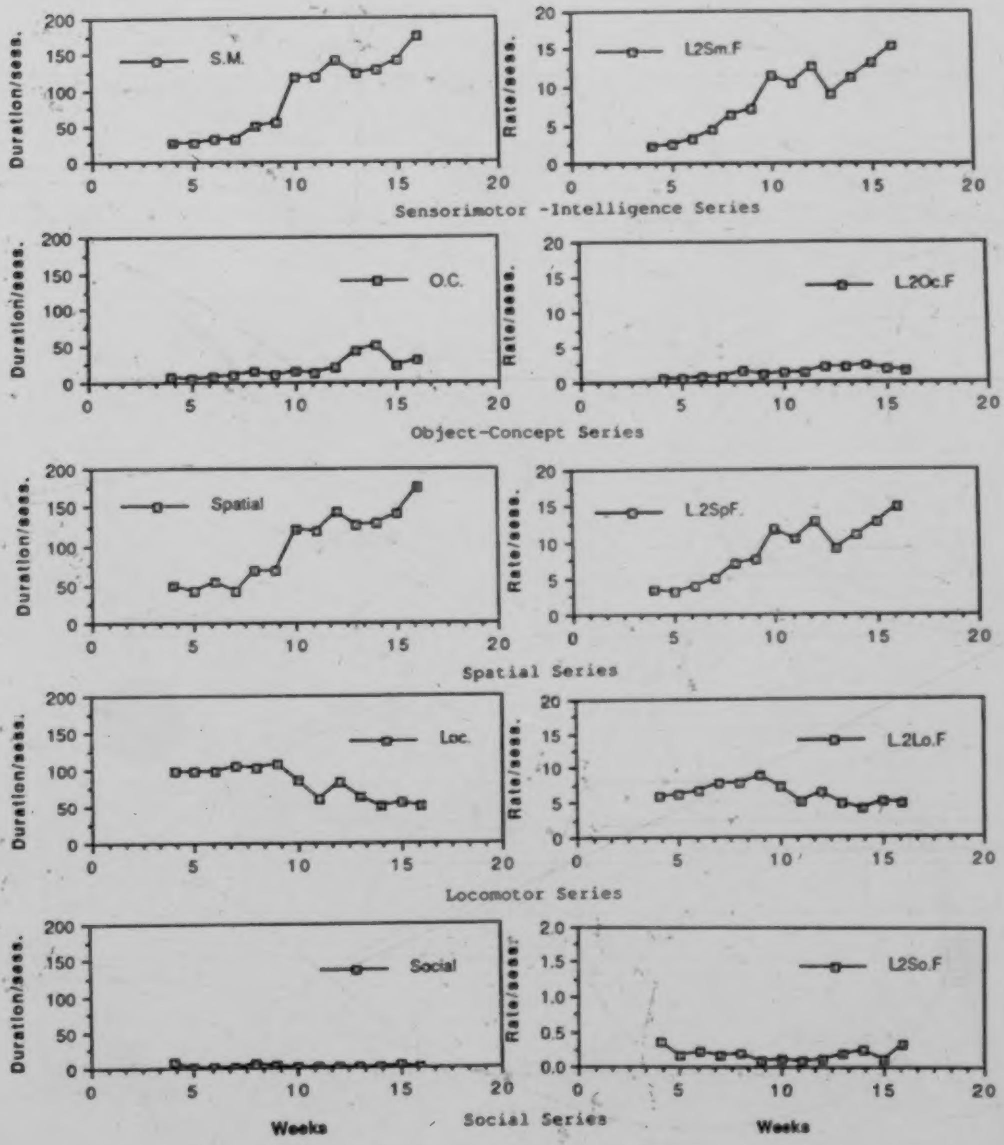


Figure 5.17. The average durations (in seconds) and rates per 10 minute session of the combined Stage 2 critical behaviors of the *Lemur catta*

Spatial Series - The high levels of activity in spatially-oriented behaviors reflected the time spent surveying the surroundings. This pattern is indicated by the almost complete overlap of the behavioral patterns in the sensorimotor-intelligence and the spatial series.

Locomotor Series - The Stage 2 locomotor actions remained an integral part of the activity patterns until the infants were 12 weeks old, when the Stage 3 locomotor behaviors typical of adult nonhuman primates began to dominate their movements.

Social Series - Very few Stage 2 social patterns (muzzles) were in evidence by the 4th week of life, as the infants had progressed to Stage 3 socially-directed interactions.

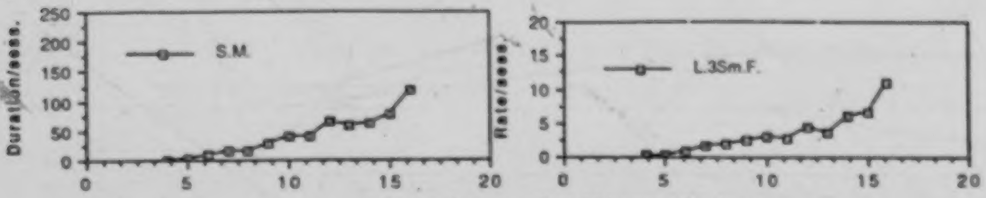
Stage 3 (Figure 5.18.)

Sensorimotor-intelligence Series - Although the infants were capable of grasping environmental objects efficiently from the beginning of the study (the fourth week of life), they were not exercising this ability to any great extent until they began self-grooming with their tooth combs.

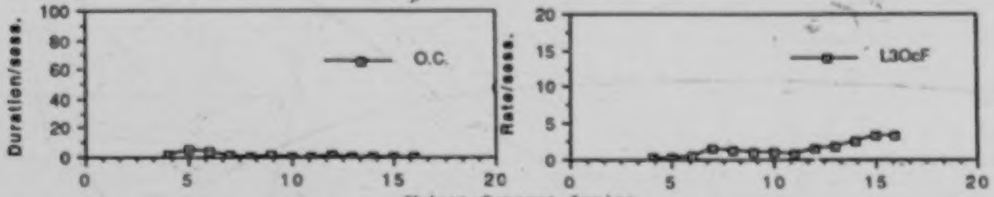
Object-concept Series - Their ability to grasp objects without groping was obvious from the beginning of the study. Although their behavior patterns indicated the ability to perceive the existence of objects that could be acted upon, the use of this ability remained at a minimal level, confined mainly to picking up small food items.

Spatial Series - The spatial component of the infant lemurs' activities was especially evident in their Stage 3 behavior patterns, especially the period between eight and ten weeks of age. This component reflected a combination of dorsal riding and independent locomotion. By week twelve, independent locomotion had taken over the spatially-oriented activities, as witnessed by the similarity between the patterns of usage in the spatial and locomotor series.

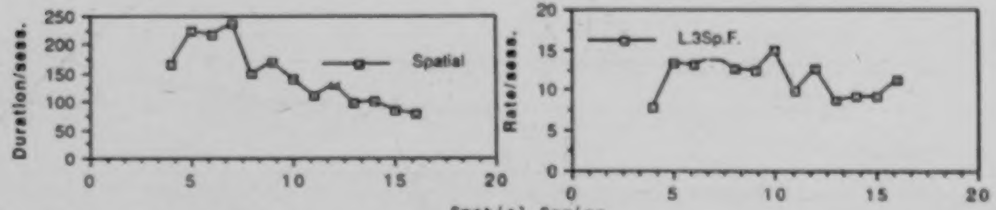
Locomotor Series - The infants were capable of the full range of basic lemur locomotor patterns (quadrupedal running and climbing) by their fifth week of life; however, the



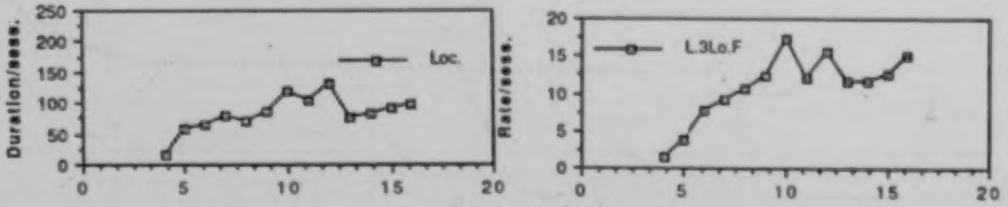
Sensorimotor -Intelligence Series



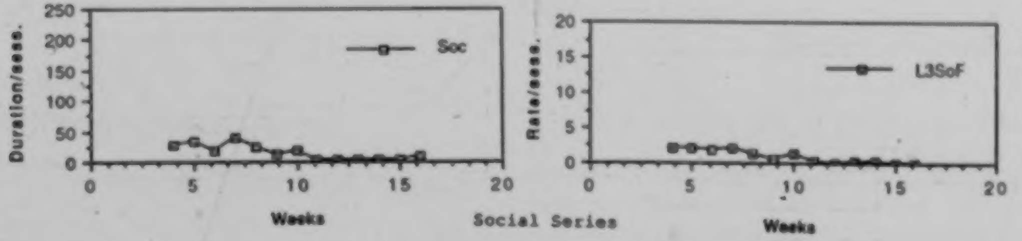
Object-Concept Series



Spatial Series



Locomotor Series



Social Series

Figure 5.18. The average durations (in seconds) and rates per 10 minute session of the combined Stage 3 critical behaviors of the *Lemur catta*

increasing confidence and skill in locomotion could be assumed by the gradual rise in the levels of duration and rates of behaviors in this series.

Social Series -The amount of time spent in socially-directed Stage 3 behaviors never reached a very high level compared to the sensorimotor-intelligence, spatial, and locomotor series. Interactions with both physical objects and conspecifics did not seem to be the young lemur's preferred activities at this stage.

Stage 4 (Figure 5.19.)

There was some evidence that the young lemurs were capable of goal directed Stage 4 behaviors in all developmental series in their first 16 weeks of life; however, the sensorimotor-intelligence and object-concept patterns were rarely used. It is unlikely that this inattention to physical objects was a function of the scarcity of stimulating objects in their enclosure, as *L. catta* in the wild seldom manipulate environmental objects (Jolly 1966).

Spatial and Locomotor Series - There was a complete overlap in the behavior patterns displayed in these series, as all of the spatially-oriented activities were linked to locomotion. The sporadic nature of these behaviors can be seen in the relatively high rates compared to the low duration of time spent in these actions.

Social Series - The pattern of socially-directed Stage 4 behaviors was the reverse of that seen in the spatial/locomotor series. Figure 5.19 shows clearly that, although the rate of social behaviors was relatively low, the infants were spending increasingly more time interacting, primarily with each other in locomotor and rough and tumble play.

Stage 5 (Figure 5.20.)

The only evidence of trial and error experimentation was in the social dimension. When the infants were 13 to 14 weeks of age, they began to display some planned social actions towards the other infants and females, primarily agonistic behaviors. At this point a maternal rejection would trigger either a bout of grooming on the part of the infant or a retaliation in the form of bites and cuffs, The fact that this level of functioning was a relatively new acquisition could be the reason that the levels of duration and the rates of Stage 5 behaviors were very low in the 16th week of life when the study concluded. Adult *L.catta* show a wide variety of agonistic behaviors in daily intra-troop activities, and also in encounters with other groups of conspecifics (Jolly 1966, Budnitz and Dainis 1975), so it is likely that the use and variety of these types of behaviors would increase as the young lemurs approached adulthood

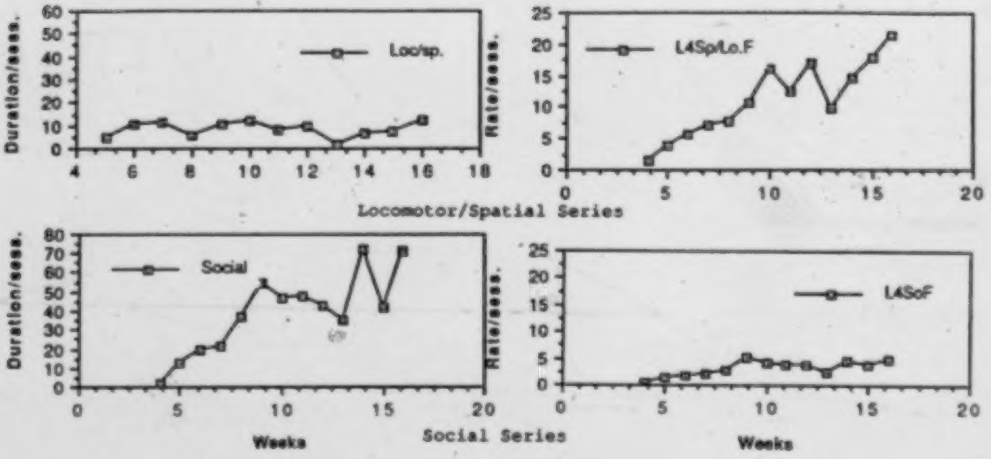


Figure 5.19. The average durations (in seconds) and rates per 10 minute session of the combined Stage 4 critical behaviors of the *Lemur catta*

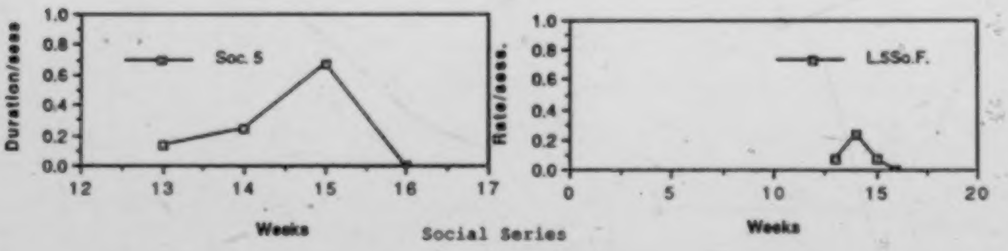


Figure 5.20. The average durations (in seconds) and rates per 10 minute session of the combined Stage 5 critical behaviors of the *Lemur catta*

Discussion: A Comparison of Developmental Patterns of the *Lemur catta* and the Cebus Infant

There were well-defined patterns in the stages of *L. catta* development which could be expected to be consistent over all infants. Clearly comparisons between species that are as widely separated phylogenetically as Prosimii and Anthroipodea are difficult to make. However, there are some developmental patterns in the infant lemurs that could be compared to those of the young cebus monkey in relation to the following factors:

a. Rate of Development - Prosimian infants are noted for their precocity and rapid maturation rate compared to the young of other nonhuman primate species, and *Lemur catta* infants are no exception (Schultz 1969, Watts 1990). It has been reported that by 16 weeks of age, young ringtailed lemurs in the wild are often exhibiting a great deal of independence in locomotion, foraging, and social activities (Gould 1990). The infant cebus monkey developed at a much slower rate, particularly in the locomotor dimension (Figure 5.21.), which was to be expected, given the difference in maturation rate of prosimians over anthropoid species and dissimilarities in habitat use. *L. catta* are the most terrestrial of the Madagascar lemurs, while the cebus monkeys spend most of their time in the upper and middle canopy of the trees (Budnitz and Dainis 1975, Fleagle et al.1981).

Although the young lemurs had achieved the early stages of development (Stages 2 and 3) by week four when the study began, the week that the critical behaviors characterizing these stages appeared could be postulated from the results of other studies (Klopfer and Boskoff 1979, Gould 1990). There was an interesting difference in the developmental patterns of the lemurs and the cebus monkey in the time lapses between the acquisition of Stages 3 through 5 in the lemur and cebus infants. In the lemur there was a relatively lengthy period between the appearence of Stages 4 and 5 (seven weeks) compared to that between Stages 3 and 4 (two weeks).

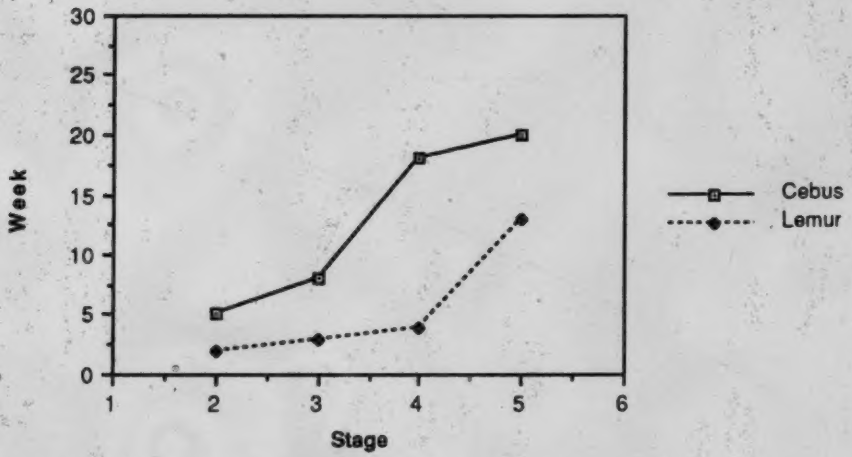


Figure 5.21. Comparisons of the weekly acquisition of developmental stages of the infant *L. catta* with that of the cebus monkey infant

The developmental pattern in the cebus monkey was very different in that 11 weeks elapsed between the beginning of Stage 3 and four behaviors, after which the infant progressed to Stage 4 in only two weeks (see Figure 5.21.). Schultz (1969) demonstrated that lemur infants mature more rapidly than anthropoid young, based on the timing of dental eruption and epiphysial union. Watts (1990) found that newborn cebus monkeys were relatively immature compared to other species of monkeys in terms of the number of centers of ossification present at birth. Therefore it was not surprising that the infant lemur developed much more rapidly in the early weeks of life. The longer period of maturation observed in the infant cebus monkeys possibly provides them with a later advantage in terms of the development of cognitive constructions with the environment, and practise in the use of more complex manipulative abilities (Antinucci 1990).

Certainly the physical precocity of lemur infants allows them little time to perfect manipulative abilities.

b. Habitat Use - One of the most striking differences in the developmental patterns of the infant lemurs and the young New World monkey was the early appearance of independent locomotion in the lemurs. Young lemurs are reported to leave their mothers in the second week of life (Gould 1989), and be fully capable of independent locomotion at four weeks of age. In contrast, the infant cebus did not even leave her mother's side until she was 12 weeks of age. By week five, the lemur infants were able to run, climb, and complete short jumps, while the cebus infant required 18 weeks to reach this level of locomotor competence. An important contributing factor is the semi-terrestrial nature of *L.catta* as opposed to the arboreal life-style of New World monkeys. The young lemurs spent most of their time in the early weeks of life near or on their mothers,who almost always rested on the ground. The cebus monkey infant had to remain in contact with her mother, well above the ground, until she had reached Stage 3 and had become confident of her ability to grasp the bars.

c. Allomothering - Although I did not observe the first few weeks after birth, it has been well documented that infant *L.catta* leave their mothers for short periods in the second week of life, and also that they are the object of transfers to other females at this early stage (Jolly 1966, Wilkerson and Rumbaugh 1979, Gould 1989). By the fourth week of life, when the infants were spending more time away from their mothers, the pattern of sitting close to other females and riding on their backs was well established.

Allomothering appears to play an important role in *L.catta* society, as the mothers are very permissive and allow other females early access to their infants. It is not unusual to see females carrying one infant and their back and another one on the ventrum or even suckling two infants. Although the young cebus monkey was muzzled and groomed frequently by the other females, she did not gain access to their bodies until she was 12 weeks of age and able to achieve the transfer herself. Unlike the lemur females, the other cebus females never tried to remove the infant from her mother.

d. Social cognition - It was clear that the onset of independant locomotion and the degree of allomothering are important factors in the social development of the infant. While the young lemurs were able to approach with confidence and snuggle close to the other females at an early age, the cebus infants had to be able to move about on their own on the bars before they could approach conspecifics. It was entirely possible that a female who was approached by the young cebus would reject her, a situation that rarely occurred in ringtailed lemur society. Trial and error social behaviors directed by the infant lemurs did not play a significant role in their daily lives until the escalation of locomotor play with their peers. This could be observed during the seventh week of life, when they had gained confidence in their locomotor abilities (Figure 5.22.).

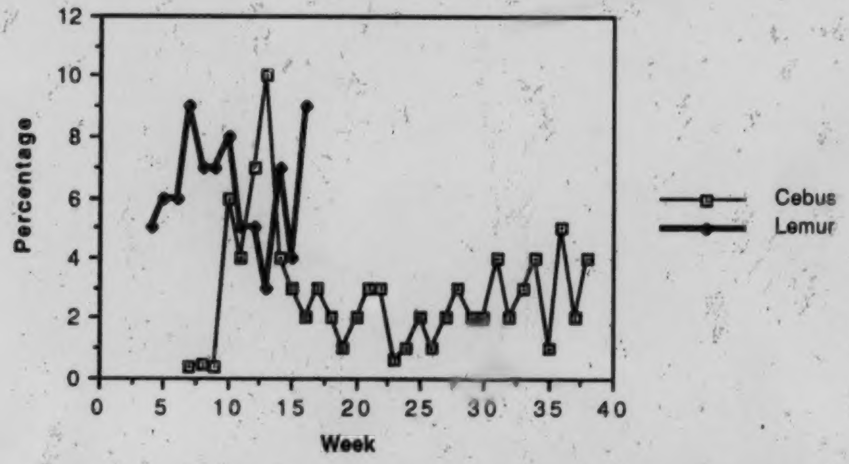


Figure 5.22. The average percentage of time per 10 minute session spent by the lemur and cebus infants interacting with conspecifics (excluding the mother)

Gould (1990) reported a similar trend in free-ranging *L.catta* infants. By the 15th week of life, the time spent in social play gradually increased to the point where it surpassed the time spent in exploration of the environment.

The social pattern of the infant lemurs and the percentage of time spent in socializing followed a very different course to that observed in the infant cebus monkey. The young lemurs gradually increased the amount of time spent in social interaction to a peak, at about week seven, after which the level fluctuated up and down. The high level of social interactions in the lemurs reflected time spent in locomotor and rough and tumble play. The young cebus monkey, in contrast, showed a peak in social interaction relatively early in its development (Stage 3), after which the time spent in socializing dropped dramatically as the tendency to interact with environmental objects became the dominant part of its behavioral repertoire. The degree of development and use of social skills in the young *L.catta* exceeded the development in the non-social domain to a much greater extent than in the young cebus monkey. By the 16th week of life the only Stage 5 behavior patterns observed in the lemurs were social in nature, and social locomotor play had become very prominent in their activity patterns. Although the young cebus monkey was fully capable of purposeful social actions, such as presenting for groom and double threats and displays with her mother, she did not use these, or even less sophisticated social behavior patterns, to any great extent later in the study.

e. Object manipulation - The activities related to objects in the environment that were so evident in the cebus infant were rarely observed in the young lemurs. This difference was not a function of the lack of stimulating objects in the zoo environment because both species in the present study were housed in similar enclosures in terms of manipulable objects. The young cebus monkey fiddled, pulled, and probed into all of the structures in her enclosure, activities that were never observed in the lemurs. These different behavioral tendencies in both cebus monkeys and *L.catta* are well documented in studies of captive and free-ranging animals (Jolly 1966, Fleagle et al.1981, Westergaard and Fragaszy 1985, Jolly 1988, Fedigan 1990).

Summary

Not surprisingly, the lemur infants developed in every area much more rapidly than the young cebus monkey. This precocity could be attributed, in part, to the early maturation of prosimians in general compared to anthropoid species (Schultz 1969, Watts 1990). However, the very striking difference in the rates of the development of the basic nonhuman primate locomotor skills of quadrupedal running and climbing in the two species was in part is a function of their fundamental life styles. *L. catta*, unlike the arboreal cebus monkeys, forage in the trees, but make their daily progressions and often spend their resting periods on the ground (Gould 1989). Thus it was relatively easy for the young lemurs to move away from their mothers while they were still unsteady on their feet. The cebus infant, whose longer period of dependence on a mother who moved almost entirely in the upper areas of the enclosure, was not able to leave her side without sufficient muscular control.

When observing young lemurs and cebus monkeys after they had reached the Stage 4 level of purposeful behavior, one cannot help but be struck by the their completely different activity patterns. The lemurs spent most of their waking hours whirling around their enclosure, chasing each other or just running, hanging, and leaping. The cebus infant, who admittedly did not have any peers to play with, spent an inordinate of time fiddling with the padlocks, sorting through the food boxes, or trying to tear down the wooden shelters in the enclosure. The lack of secondary and tertiary circular reactions so evident in young children was particularly striking in the infant lemurs. In contrast to this, the cebus infant did exhibit a degree of repetition in her actions directed towards environmental objects.

As with the other species, socially-directed behaviors of any consequence did not appear until Stages 3 and 4 had been achieved, but in the case of *L.catta* this was very early in life (weeks four to five). From this point on there was an expansion in the use and variety of social behaviors, especially those directed towards peers. Locomotor play evolved over the weeks from a series of chases to a bewildering variety of actions carried out at breakneck speed. These actions include leaping on one another, wrestling with one or more partners while hanging from the branches by the hands or feet, cuffs, and play bites. By the 14th week of life, the young lemurs were exhibiting more adult social patterns principally in the form of agonistic interactions and grooming with the specific intent to affect the behavior of others. This was particularly noticeable with their mothers,after the weaning process had begun. It was interesting to note that, despite the semi-terrestrial propensities of *L.catta*, the young lemurs' play took place almost entirely in the branches.

In summary, the young lemurs' rapid rate of development was typically prosimian, as they had achieved Stage 4 in all areas by the fifth week of life. Although the abilities at 16 weeks of age did not indicate the degree of behavioral flexibility with physical objects shown in the young cebus monkey, the social actions were rapidly increasing in sophistication.

When discussing lemur cognitive abilities, it has been common to describe them as "less intelligent" than anthropoid species.It appears that the cognitive development of *L. catta* and the cebus monkey runs a similar course in the early stages (1 through 3). The cognitive development in the subsequent stages should be described as "different from" rather than "less than" that of the cebus monkey (Wilkerson and Rumbaugh 1979). In terms of physical object-concept and object manipulation, the lemurs did not show the behavioral flexibility of the young cebus; however, in a social sense, their behaviors were of comparable sophistication. In lemur society, perhaps the daily pressures of living in a complex social group selected for the greater expansion of cognition in the social domain.

Chapter 6. General Discusssion and Conclusions

Interspecific Comparisons of the Development of Social Cognition In Four Nonhuman Primate Species

Parker (1990:47), in an extensive discussion of comparative developmental studies that address the cognition of primates, stated that " it is already clear from the limited comparative data available that the taxonomic distribution of mental abilities does not fit a simple grade-level model". The comparison of the cognitive abilities of primate species that are distantly related phylogenetically, or even ones that belong to the same family, is frought with difficulties because of a number of factors, which include differences in the selective factors operating on the animals, and dissimilarities in structural organization (Parker 1990). However, I suggest that the following interrelated biological and contextual factors contributed in part to the variability in the rate and extent of cognitive development observed in the comparisons bteween the cebus, squirrel, and patas monkeys and the ringtailed lemurs.

Rate of Development

Schultz (1969) demonstrated that there was a clear trend in the maturation rate within the Order Primates, based on the timing of dental eruption and epiphysial unions. His evidence indicated that lemurs mature more rapidly than anthropoid species; and that this trend can also be seen in the Anthropoidea, with cebids maturing more rapidly than cercopithecoids, and monkeys maturing more rapidly than apes. It was predicted that if the rate of prenatal ossification was slowed as the rate of gestation increased, one would expect to find more centers of ossification at birth (as an indicator of skeletal maturity) in cebids than cercopithicoids, and more in the latter than in apes (Watts 1990). In other words, cebids would be more mature at birth in terms of skeletal development than cercopithicoids.

However recent research on the centers of ossification present at birth has shown that these trends are not at all clear. Watts (1990:94) records data from a number of sources that show squirrel monkeys to be more mature than cebus monkeys at birth, despite their membership in the same family of New World monkeys and similarities in gestation time. More surprisingly "despite the trend for increasing gestation time, the skeletal development of rhesus macaques is markedly advanced compared to other groups" (Watts 1990:94). Workers in primate nurseries report the same trend of advanced neuromotor maturation in infant macaques over newborn squirrel and cebus monkeys (Watts 1990). Watts (1990) suggested that perhaps this trend for precocity in skeletal development in infant macaques is a derived feature that may be present in all cercopithecoids.

Given the evidence that prosimian infants are generally more precocial than anthropoid young, it was surprising to note similar levels of early development in the young lemur, the squirrel monkey and patas monkey. The patterns and timing of early development in the infant lemurs, patas, and squirrel monkey were strikingly similar. Although the development of independent locomotion in the infant squirrel monkey was slower than that of the other two species, the appearance of the ability to attend to the environment and to grope for objects typical of Stage 2 occurred within the first weeks of life. This is possibly related to the relative skeletal maturity of squirrel monkey infants at birth (Watts 1990); and also to the dorsal position of the neonate on its mother, which would facilitate an early view of the world and provide an opportunity to gain a tactile knowledge of the substrate. The precocity of the infant patas monkey could be an indication of the skeletal and neuromotor maturity seen in newborn macaques and possibly all cercopithecoids (Watts 1990). It has been suggested that the precocity of patas infants is an adaptive response to life in an extremely harsh environment, where an early maturation in physical and social abilities would improve chances of survival (Chism 1986). A comparison of developmental patterns indicated that there was a greater similarity between those of the lemur infants and the young patas and squirrel monkeys than between those of the two New World monkey infants (Figure 6.1.)

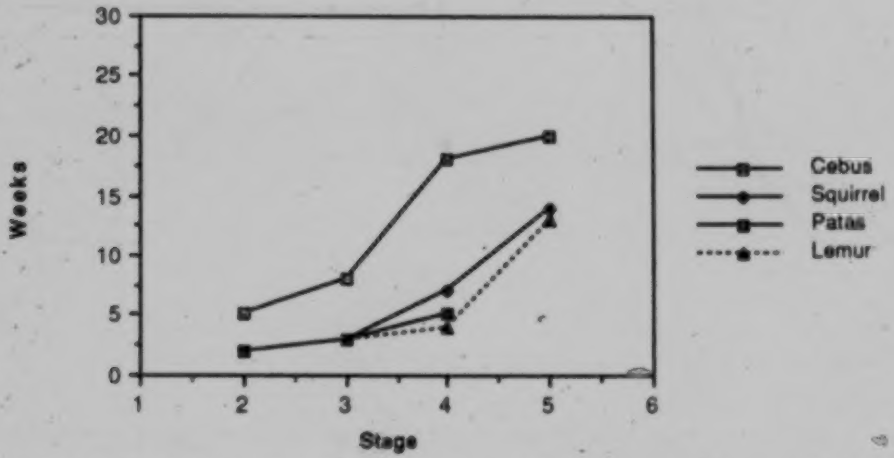


Figure 6.1. Comparisons of the weekly acquisition of developmental stages in the infant L.Catta, Cebus, squirrel and patas monkeys.

The role of the relative precocity of the infants was obvious in the early appearence of Stage 3 behavior patterns in the social series. The lemur, patas, and squirrel monkey infants began to direct their attention to their conspecifics, indicating the beginning of the concept of social object concept fully four weeks before the young cebus monkey (see Appendix 2). The cebus monkey spent a considerably longer period clinging to her mother before attending to the physical and social environment. The Stage 3 social patterns, once achieved, became prominent in the cebus infant behavioral repertoire. By the time this infant reached the Stage 4 level of development, however, she exhibited a greater degree of flexibility in the manipulation of objects in the physical environment than was apparent in the other subject species.

Although the two New World species, the patas monkey, and the lemurs studied are widely separated taxonomically, their cognitive development appeared to follow similar patterns in the social and non-social domains in the early stages. In Stage 2 the concept of object permanence was similar in both dimensions, with the infants showing an inability to grasp any idea of the constancy of social or physical objects; and the use of these behaviors remained at low levels. The patterns of usage of Stage 3 behaviors were also similar in the four species. The infants were now aware of the existence of objects to the extent that they could be acted upon. Although they exhibited a whole new repertoire of behaviors towards physical and social objects, newfound locomotor skills dominated their activities. From the beginning of Stage 4, the infant's species-typical propensities became more evident; and the association between the cognitive development in the social and non-social dimensions appeared to weaken.

In the cebus monkey, the indication of this weakening was not seen until the last weeks of Stage 4, when the use of more complex manipulative abilities was much more evident in interactions with the physical environment. The infant squirrel monkey showed a very different pattern of activity with social compared to physical objects. The duration of time spent in Stage 4 social activities exceeded that spent in object manipulation, while the opposite situation could be observed when looking at the rates of behaviors in the respective series. The frequency of interactions with physical objects could be related to the squirrel monkeys' restless, mobile style of foraging and feeding in the wild whereas social activities, such as rough and tumble play, tend to be more prolonged in duration. In the young lemurs, there was a striking difference in the levels of Stage 4 behaviors in object-concept and social series in that the values were so low in the former series that they could not be recorded on a graph. This result was not surprising, given the behavioral tendencies recorded for *L.catta* in the wild where it is well documented that ringtailed lemurs are very active socially, while spending very little time in physical object manipulation (Jolly 1966, Jolly 1988). Since the study was concluded just as the young patas monkey had begun to use Stage 4 object-concept behaviors, little can be said about the relationship of Stage 4 social and object-concept behavior patterns. However, the use of Stage 4 social behavior patterns increased abruptly during the seventh week of life when the study concluded, indicating that the social precocity recorded in the literature for patas monkeys was evident in the infant in the present study.

Habitat Use

There was a marked degree of diversity in the habitat use in the four species, with the cebus and squirrel monkeys being highly arboreal compared to the predominantly ground-dwelling patas monkey and the semi-terrestrial lemurs. The terrestrial proclivities versus the arboreality of the subject species was a major factor in the speed with which the infant's skills developed, particularly in the spatial, locomotor, and social dimensions. The greatest similarity in the developmental patterns of the infants could be seen in the first two stages. The involuntary, reflex motor actions that were characteristic of the first stage began to come under greater muscular control in Stage 2. The most obvious differences in the rates of development of the four species was the timing of the onset of independent locomotion, which was clearly related to the habitat use. In the arboreal New World species (the cebus and the squirrel monkeys) the acquisition of Stage 3 locomotor skills (branch running and climbing) lagged well behind similar skills in the lemurs and the patas monkey. The former infants were not able to venture from their mother's side until the ability to coordinate vision and prehension was well established, while the semi-terrestrial patas and lemur infants were able to move away from their mothers well before they had developed hand-eye coordination.

The relationship between the onset of independent locomotion and habitat use was much more striking in the present study than in other research using the Piagetian model with a response-elicited regime. An infant cebus monkey tested on a laboratory floor or table would not have the same constraints on movement as one living in the trees or bars. Antinucci (1990), in his comparison of the cognitive ontogeny of cebus, macaques, gorillas, and human infants, found that the relationship between the development of object-concept and the onset of independent locomotion appeared in the acquisition of Stage 2. However, in the present study, the squirrel monkey achieved the Stage 2 in the object-concept series; and was able to attend to, and grope for, objects long before he was capable of independent locomotion. This is likely due to the fact that newborn squirrel monkeys are more mature skeletally than cebus monkeys; and cling to the dorsal surface of their mothers, giving them an advantage in spatial orientation over the ventrally clinging cebus infants.

The capacity for independent locomotion was particularly critical in the timing of the development of social cognition. In semi-terrestrial species like patas monkeys and *L. catta*, the infants did not have to wait for a social approach but could move towards their conspecifics at an early age. The social maturation of these species was also facilitated by the high degree of allomothering in the early weeks of life, as the infants were familiar with other females in the social group and were less apprehensive about approaching them. Antinucci (1990:167) suggests that "The onset of independent locomotion channels interaction with the outside world in a physical and social sense".

General Remarks

In each of the case studies, the first intentional socially-directed behaviors (Stage 3) appeared shortly before those in the other series. In the lemurs, more so than in the other species studied, the disparity in the levels of acquisition and use of socially-oriented and non-social activities was particularly striking. Compared to cebus and squirrel monkeys lemurs, as a rule, score very badly on intelligence tests administered in laboratories, particularly on those tasks concerned with the discrimination and manipulation of objects (Jolly 1966, Wilkerson and Rumbaugh 1979). Jolly (1966) argues that this difficulty could have as much to do with their unwillingness to do the test as with their ability to learn, since research indicates that *L.catta* in both captive and free-ranging situations show little inclination to manipulate objects. However *L. catta* are highly gregarious animals whose social organization is as complex as that seen in most monkey species.They display a complete repertoire of social interactions including allomothering, social play, extensive grooming, and agonism in competition for resources and territorial defence. Studies report the existence of dominance hierarchies in both male and female *L.catta*, and the young members of the social group must learn their relative rank as well as how to deal with kinship relations and the idiosyncracies of their conspecifics (Jolly 1966, Budnitz and Dainis 1979, Wilkerson and Rumbaugh 1979). The major difference between the social behaviors of lemurs and anthropoid species is the prosimian style of grooming, which is done almost exclusively with the tongue and dental comb instead of the hands (Jolly 1966). The disparity in the levels of acquisition and use of socially-oriented and non-social activities was particularly obvious in the *L.catta;* more so than in the other species studied. The use of the behavior patterns characteristic of the later stages of cognitive development in ringtailed lemurs appears to be highly specific to the social dimension.

The infant patas and squirrel monkeys were also very social animals; however, the striking difference in the early social behaviors of the lemurs compared with that of the other species was the inordinate amount of grooming and allogrooming on the part of the young prosimians. This could be a reflection of the fact that lemurs groom with their tongues and dental combs a practice which requires less coordination than manual grooming. The young squirrel monkey never did attempt to groom another animal throughout the 20 week study, which is not surprising given the fact that grooming in this species is a relatively rare occurrence. The sociability of the young squirrel monkey was more a reflection of his increasing tendencies to spend time closely monitoring the activities of others. This could be a species-typical behavior pattern, as Fragaszy (1985) reports the inclination of adult squirrel monkeys to keep close track of each other. The patas monkey was perhaps the most socially inclined of all the infants, as the average amount of time per session spent interacting with the other females remained at a comparatively high level throughout the short six week study. While the other species became extremely active in a locomotor sense once they were able to move away from their mothers, the young patas monkey used his new-found skills primarily to expand his social horizons.

The cebus monkey was the least socially-oriented animal in the later stages (4 and 5) of development, although clearly the infant was capable of these levels of social behaviors. At this point the species-typical penchant for manipulating environmental objects took over, and these behavior patterns became predominant in her daily activities. Early in Stage 3, before the cebus infant had begun to locomote with confidence, social interactions with the females in the social group made up a very important part of her behavioral repertoire, although ultimately the relative importance of social activities in daily life was overshadowed by manipulatory activities.

Keeping in mind that these species are not all from the same phylogenetic category, there are differences in the rates of development and expression of social cognition that could be attributed in part to the factors suggested at the beginning of this chapter. Certainly the relative rates of physical maturation, the style of habitat use, and also aspects of social patterns such as the degree of allomothering figure prominently in interspecific comparisons of the development of social cognition. In the final analysis, the primate species that exhibited the greatest use of social skills were the semi-terrestrial patas monkey and the ringtailed lemur, whose rapid physical maturation and early exposure to other females in the group facilitated their development in the social domain. It could be predicted that the same rate of social precocity and expression of social cognition would occur in other primate species where all these factors are coincident. Although clearly there will be individual variability in cognitive development, in order to investigate other contextual factors affecting intraspecific differences in social cognition, further comparative studies would have to be done on primates living in the wild and in a variety of captive social groupings.

The small sample sizes in the present study made it impossible to address differences in the cognitive development of male and female infants. Antinucci (1989a) and his colleagues at the Instituto di Psicologia in Rome did not discuss sex-related differences in the development of object-permanence in their recent publication presumably for the same reason; however, any variability would likely be more apparent in interactions with the social as opposed to the physical environment. There are behavioral differences in adult male and female animals, but there has been no suggestion of sex-related differences in the ability to understand relationships or to use social strategies. Fedigan (1982) discussed sex differences in behavior and suggested that the lack of evidence has prevented primatologists from knowing at which developmental stage these behavioral differences appear. There are some reports that infant males behave differently from females but in many cases the evidence is conflicting (Fedigan 1982). Moss (1974) found minimal sex-related differences in behavior in very young human infants; however, the expectations of the parents and others are not the same for boys and girls as they grow up, a factor which could be expected to contribute to the behavioral differences seen in older children. The comparison of the acquisition and use of social cognition between male and female nonhuman primate infants, would be an important addition to our knowledge of primate cognitive development.

It is important to note that, although nonhuman and human primate infants move through the Piagetian developmental stages in a similar fashion, gradually acquiring the concept of the permanence of social and physical objects, there are striking differences in the types of behaviors exhibited. Parker (1977) and Antinucci (1989e) noted that infant monkeys do not exhibit secondary or tertiary circular reactions, which are repetitive behaviors directed towards objects, or in object-object coordinations. Field and laboratory studies have indicated that cebus monkeys and chimpanzees are exceptional in this respect in that thay show a degree of circularity in their manipulation of objects, and use objects to act on other objects (Parker and Gibson 1977). Parker (1977) suggested that the secondary and tertiary circular reactions observed in children in social and non-social contexts are critical in the developmental process. They provide the basis for the ability to deal appropriately with the physical environment as well laying the foundation for language acquisition and the formation of a self-image. Antinucci (1989e) argued that the major difference between human and nonhuman cognition is not simply that the organizational structures do not develop as far in nonhuman primates, but that the mode of development is very different. The research conducted by Antinucci and his associates at the Instituto _di_ Psicologia in Rome has indicated that nonhuman primates are able to grasp logical operations allowing them to achieve a goal; however, they fall behind human infants in the ability to understand the physical properties of the objects they are manipulating (Antinucci 1989e). Antinucci speculated that this could be related to the lack of secondary and tertiary circular reactions which provide the human infant with a more complete knowledge of the social and physical world (Antinucci 1989e).

An argument could be made from the results of the four case studies of primate development that there is a close association in the expression of social and non-social cognition in very young primates which tends to disappear, or at least weaken, as the animals approach maturity. In some cases, the development of abilities in the social dimension surpasses those in the non-social domain. The final section of this chapter will pursue this argument using the case studies discussed in Chapters 4 and 5, as well as information taken from behavioral studies of other species.

The Social Primates

Anyone who has studied nonhuman primates living in social groups, or even watched them in a zoo, will have been impressed by the extent and sophistication of their social activities. Dasser (1985) suggests that primates, whose social life is characterized by a variety of individual relationships with their conspecifics, seem to surpass non-primate species in the scope and complexity of their social behavior.

Until recently, there has been a dearth of hard data that could be used to assess the extent of primate social intelligence, because of the constraints involved in this type of research. Much of the available material from the field is judged to be anecdotal and therefore inadmissible as scientific data, while laboratory studies are hampered by the scarcity of large social groups and the problems associated with setting up social tasks to be mastered (Whiten and Byrne 1988). The real obstacle in assessing social intelligence in primates, or any other animal, is the difficulty in distinguishing between problems solved by "knowing how" (the ability to associate a particular procedure with a particular situation) and "knowing that" (the ability to make inferences about cause and effect) (Cheney and Seyfarth 1990). However, in the past decade there has been an upsurge of interest in the social capacities of primates, resulting in the generation of some very creative research projects providing clear evidence that nonhuman primates have the ability to understand their own relationships, and those of others and can act accordingly (Stammbach 1988).

Some studies have made use of the fact that a number of nonhuman primate species, such as macaques, baboons, ringtailed lemurs and vervets, have clear dominance hierarchies in both males and females. As a rule, in these female-bonded species, the female hierarchies are much more stable than those of the males (deWaal 1989). Rank in nonhuman primates has proven to be a social tradition dependent on social competence rather than size or strength; and in many species, status within a group is not random but depends on the rank of the mother. The primacy of attention to dominance rank in these societies is an indication of the importance of social rules in their daily lives (deWaal 1989). In his research on aggression and reconciliation in a number of nonhuman primates (deWaal 1989) found that, although the rigid enforcement of rank varied somewhat between species, the animals in the social group had no difficulty assessing their own position in the hierarchy; and were able to adjust their interactions with other group members in the light of this assessment.

Stammbach's (1988) laboratory research with *Macaca fascicularis* addressed the ability of monkeys to recognize characteristics of others within a rank-ordered society. He trained low-ranking animals to be specialists in getting popcorn from a machine; and found that the dominant animals behaved differently towards the subordinate animals depending on whether they were active or inactive at the popcorn machine. The higher ranking monkeys curbed their usual agonistic tendencies towards lower ranking animals at a food source, and exhibited affiliative gestures in order to receive a share of the popcorn. Stammbach was able to show that the specialists and the other members of the group were able to remember their roles when he reintroduced the popcorn vending machines a number of months after the study had been concluded.

Other researchers have focussed on the importance of kin relationships in nonhuman primates. Although it is generally accepted that a number of species, primates and non-primates, are able to recognize related conspecifics, only primates have been reported to have the ability to recognize kin relationships in others. Dasser (1988) found that socially-experienced female *Macaca fascicularis* could recognize mother/offspring pairs from other pairs, regardless of the age of the offspring; and were also able to categorize social affiliations between maternal siblings and between members of the same matriline. Dasser feels that her research, which involved the recognition of animals from 35 mm slides, clearly indicated that the monkeys could classify their group members and were able to form concepts about the relationships of others.

Cheney and Seyfarth (1988, 1990) and Gouzoules (1986) have carried out a number of innovative experiments on vervet and rhesus monkeys respectively, and have come to similar conclusions about the social capabilities of monkeys. The results of their playback experiments of monkey vocalizations showed that the monkeys could distinguish between calls of kin, non-kin, and animals belonging to another group. Cheney and Seyfarth (1990) also found that the vervets could associate the playback of an infant's vocalization with the female who was its mother. Other experiments provided evidence that redirected aggression is not used randomly by the vervets, but was almost always directed towards specific individuals who were associated in some way with the monkey involved in the original agonistic encounter (Cheney and Seyfarth 1990).

Kummer pioneered experimental work in the field with studies showing the ability of transplanted female savannah baboons to adjust their patterns of social behavior to the very different female role in hamadryas baboon society (Kummer et al.1970). His subsequent research with hamadryas baboons has provided strong evidence that the animals can retain a large store of knowledge about the characteristics and behavioral tendencies of their group members (Kummer 1982).

F. deWaal (1989) found that aggression and reconciliation are major components in the social lives of a number of nonhuman primate species. Reconciliation proved to be particularly critical because of the necessity of maintaining and reinforcing kinship and other social bonds in a large troop. It was particularly interesting to note the variety of conciliatory devices used by the different species. Whereas rhesus macaques were generally very subtle in their affiliative actions towards a former antagonist, stumptailed macaques made peace in a highly predictable and conspicuous manner.

The previously mentioned research projects are among the relatively few laboratory and experimental field studies devoted to social intelligence compared to those focusing on other areas of behavior. However, many primatologists have documented anecdotes which attest to the social sophistication of their subjects. Strum (1985), in particular, reports that the baboons at Gilgil employed creative social strategies and manoeuvres requiring a great deal of finesse in order to survive in the social group. The strategies, which were different for males and females, ranged from attempts at social climbing, reconciliation and affiliation, to agonistic buffering, in which a particular infant or female would be used as shield to defuse aggression. Whiten and Byrne (1988) canvassed primatologists for examples of deceptive behavior in their nonhuman primate subjects, and have compiled them in Tactical Deception in Primates:The 1990 Database (Byrne and Whiten 1990). The fact these are anecdotal reports of infrequently observed behaviors should not detract from their validity because an often-repeated behavior would lose its ability to deceive. Some have questioned the degree of intelligence needed for withholding information or providing false information; however, it seems clear from many of these anecdotes that the primates are fooling each other with a definite goal in mind (Jolly 1988).

Mental Representations - Yes or No?

The development of object-concept has been investigated in an ever-growing number of nonhuman primate species using the Piagetian cognitive-developmental model (for a list see Natale and Antinucci 1989:98). Stage 6, the last stage in the sensorimotor period, marks an important milestone in cognitive development in that it is characterized by the use of a mental representation to achieve a goal instead of trial and error experimentation. Although many researchers have reported the successful achievement of Stage 6 in their primate subjects, Natale and Antinucci (1989) argue that the testing procedures were not sufficiently stringent to provide proof that the required tasks were completed using mental representations rather than complex associations. In their comparative study of Stage 6 abilities of cebus monkeys, two macaque species, and a gorilla, where the tasks were set up to allow the researcher to differentiate between the use of representational and non-representational responses, only the ape was judged to have representational ability (Natale and Antinucci 1989). Subsequent to this work, researchers using the same methods found that one adult cebus monkey appeared to use mental representations in achieving an object-oriented goal (Schino et al.1990).

In the present study, a social series was added to the Piagetian model in order to compare the development of cognitive abilities of nonhuman primate infants in social and non-social spheres. The criteria (critical behaviors) were chosen to indicate the attainment of abilities in social object-permanence. None of the infants showed any evidence of the use of mental representations in their dealings with conspecifics, an absence which could be a function of their immaturity since none of the primates studied were older than nine months of age. Cheney and Seyfarth (1990) argue that, in some species of Old World monkeys such as vervets, baboons, and macaques, who live in large social groups, there is evidence that the adult animals use mental representations in their social activities. The social knowledge of these primates extends to all others in the social group including their own kin, the kinship relations of others, pair bonds, and dominance relations. All of this evidence points to the fact that nonhuman primates act quickly and purposefully in their dealings with others, behaviors which would certainly place them in Piaget's Stage 6 level of cognitive ability.

Some animal behaviorists would argue that the animals are relying on complex associations through conditioning and visual discriminations rather than mental representations in their dealings with conspecifics. However, it would seem more parsimonious to say that the monkeys understand relationships and can use mental concepts in order to act appropriately, than to say that they have to learn and remember the characteristics of every interaction (Cheney and Seyfarth 1990:176). In non-primates, social strategies almost always deal with close kin like offspring, while in primates, whose social interactions often involve three or even more conspecifics, the complexity of social interchange escalates rapidly (Harcourt 1988). Since social interactions have to be assessed at different levels of abstraction, would it not seem reasonable to assume that the monkeys must have some sort of mental image of the characteristics of their group members and are using more stringent criteria than just association in the interactions (Cheney and Seyfarth 1990)?

Social versus Non-Social Cognition

The discussion concerning the social competence of nonhuman primates could lead one to question the distinction between social and non-social cognition. Developmental psychologists in the past have assumed that cognition was applicable to any domain, and Dasser (1985) still argues that there is no reason to believe that social skills are acquired by different processes than those dealing with the physical world. Recently however, primatologists and psychologists have suggested the possibility of a qualitative difference between social and non-social cognition. Seyfarth and Essock-Vitale (1987) point to the difficulties encountered in the laboratory training of monkeys to do tasks dealing with mental concepts like transitivity. Monkeys in the wild, however, seem to be able to learn their place in the dominance hierarchy (a similar concept) with very little effort. The experimental work with free-ranging vervets conducted by Cheney and Seyfarth indicates that the same animals who are so adept at picking up social cues seem unable to use physical cues to alert them to the presence of a predator (see Cheney and Seyfarth 1990:288-289 for details of the experiment). This is not to suggest that the socially-skilled vervets are lacking abilities in all other areas, only that cognitive abilities may be farther developed in the social arena.

The present study shows that the social series in Piagetian Stage 3, the first truly social stage, began somewhat earlier than the non-social series in all of the species regardless of differences in habitat use or precocity. Presumably this pattern would be especially true in the wild where larger groups would provide more opportunities for peer group interaction. Likely the feedback derived from the multiplicity of interactions would supply the stimulation necessary to promote enhanced social skills. This type of feedback would not be available from activities carried out on inanimate objects.

Research carried out on human infants has shown that the concept of person-permanence often appears before that of object permanence (Smith 1988). Although the disparity is less noticeable when familiarity and differences in methodology are controlled for (Jackson et al.1978), Smith (1988) argues that in real life situations, interest and familiarity with social stimuli are often an integral part of an infant's development, and are difficult to control. A secure attachment bond with the mother has proven to facilitate the development of person permanence, and to favor a precocity in social compared to non-social contexts (Smith 1988). The importance of "contingent responsiveness" (Smith

1988:97) in the development of social cognition of human infants, in which the child receives a positive response to its behavior at an appropriate time, could also hold true for nonhuman primate infants. For example, a human mother would pick up and comfort a crying infant, while a monkey mother would retrieve a distressed infant and allow it to suckle.

In 1966, Jolly published her landmark paper, "Lemur social behavior and primate intelligence", in which she used her data from research on wild Malagasay lemurs to promote her thesis that social agencies were likely prominent in the evolution of primate intelligence. She found that *Lemur catta* in the wild or in captivity were not active or particularly creative in terms of their manipulation of physical objects, but did show a great deal of flexibility in their social activities (Jolly 1966). The case study of the lemur infants in the present project was particularly revealing. The infant lemurs progressed to the Stage 5 level of cognitive ability only in the social dimension; and were extremely gregarious individuals at 16 weeks of life, when the study was concluded.

The ability to understand the permanence of social and physical objects followed similar developmental patterns in the early stages in all of the study species. The durations and rates of the Stage 2 behaviors in the object-concept and the social series never reached a very high level, since these behaviors pertained to the level of development at which the infants had no concept of the permanence of objects. The appearance of Stage 3 behaviors patterns and the newfound ability to coordinate vision and prehension ushered in a whole new cognitive dimension which included a rudimentary awareness of the constancy of environmental objects and conspecifics within the infants' sphere of activity. At this point, the use of these new behavior patterns increased rapidly, reached a peak, and then decreased as they were partially replaced by more complex Stage 4 behavior patterns. The infant lemurs proved to be an exception at this point because, although they showed some degree of Stage 4 capabilities in their interactions with environmental objects, they primarily used the Stage 3 level of manipulatory activity.

Once the Stage 5 level of cognitive development was achieved and the existence of an object was no longer tied to the context in which it was seen, the association between the development in social versus non-social object permanence was much less obvious. At this point the species-typical propensities appeared to dictate the major activity patterns in the young animals, who were just approaching adult levels of behavior. Hinde (1985) suggested the possibility that certain cognitive prerequisites need to be in place before the differences in some aspects of social and non-social cognition appear.

Antinucci and his associates at the Instituto di Psicologia in Rome conducted a number of detailed experiments comparing the cognitive development of primates using the Piagetian model (Antinucci 1989a). They tested macaques, cebus monkeys, and gorilla infants and adults in the development and use of object-concept abilities and compared the results to those reported for human infants. They found that cebus monkeys fall between the macaques and human infants in terms of their manipulatory skills. Cebus infants show more secondary circular reactions (repeated actions carried out on an object) than the gorilla or macaque infants, but in a less creative way than human infants (Antinucci 1989d). Cebus infants showed consistently higher scores than macaques in object manipulation, and also appeared to have a better grasp of cause and effect in their ability to retrieve items with a stick (Natale 1989a, Natale 1989b). Poti and Antinucci (1989) established criteria for first and second order cognitive constructions in order to compare the logical abilities of the four primate species. First order constructions involved the ability to put together a set of two or more objects based on some characteristic, such as color or shape. Second order constructions referred to the ability to construct sets of sets, where a set of objects is seen to be related to another set based on some common characteristic. Cebus monkeys were able to use second order cognitive constructions in their dealings with objects, while the macaque species never advanced past first order capabilities.

It would appear from the wealth of material attesting to the social attributes of macaques, baboons, and vervets, that Old World species are quite capable of second order constructions in their social lives. The ease with which these primates successfully deal with their own kin, the kinship relations of others, and dominance hierarchies on a daily basis strongly indicates a well-developed ability to construct different sets of conspecifics based on social characteristics. Referring to the species used in the present research, it could be predicted from the results that the squirrel monkey, the lemurs, and possibly the patas monkey would also rank below the cebus monkey in their ability to handle second order constructions with objects; but would be fully capable of these cognitive constructions in the social arena. The cebus infant, although she had clearly achieved the same level of social capability as the other infants, was the least socially-active of any of the other primates. Cebus in the wild move in widely dispersed social groups and are not noted for their sociability (Terborgh 1983), so it would seem that their creative energies are expended primarily on their interactions with the physical environment.

Could it be the case that a number of nonhuman primate species, particularly those who live in large cohesive social groups, show a lesser degree of skill in their actions with physical objects than in their social activities?

The Evolution of Primate Intelligence

Harcourt (1988:111) asks, " What are primates doing with their large brains and superior intelligence that non-primates are not?". He argues that the environments and diets of primates are no more complex than those of non-primate species, and superficially the primate social environment does not appear to be more complex. However upon closer inspection, it could be noted that primates _do_ have more complex types of social interactions, primarily those related to alliances and three-way interactions which are frequently seen in primate societies and much more rarely in other species.

As discussed in Chapter 2, there are two main schools of thought regarding the evolution of intelligence in primates, the "ecological origin" and the "social origin" theories. Clearly some primates species, like cebus monkeys, are particularly skillful in extracting food from their environments and dealing with the practical matters of everyday life. Laboratory research has indicated that a number of species of monkeys and prosimians show rather limited abilities in forming mental concepts when dealing with objects. However, an ever-growing body of literature indicates that many species of monkeys are able to make use of similar concepts in their social dealings. The present research, which has described the development of four nonhuman primate species in social and non-social areas, indicates that the development of social object-concept precedes that of object-concept in a non-social sense in Stage 3, which signifies the emergence of systematic intelligence in the infant (Piaget 1952). In every species, except the cebus, the use of social behaviors (not necessarily the most complex ones) outweighed the levels of use of object-related behaviors.

Clearly selection for the evolution of higher intelligence in primates was not an "either-or" proposition, and both ecological and social pressures were involved. As with every question addressing the evolution of behavioral attributes, we can only deal with speculations, and make educated guesses extrapolated from the available evidence from studies of extant species. It is not possible to know the relative contribution of ecological and social factors to the evolution of intelligence in any given species. Humphrey (1976) argues that managing the practical matters of everyday life requires less mental flexibility than coping with social demands of group living, and suggested that perhaps skill in managing social situations was critical in the evolution of cognition. The problem is that we have no way of knowing if he was right or whether Milton (1988) was closer to the truth when she noted the clear association between brain size and diet which seems to suggest that the pressures of finding nutritious food were in part responsible for expanded intelligence.

Primates, whether they live in the tropical forests or the arid areas of Sub-Saharan Africa, must have a wide knowledge of their environment. Gibson (1986) commented on the fact that the large brains of primates must have proved advantageous for them or there would have been selection for a reduction in brain size. It is possible that the expansion of the neo-cortex allowed primates to become specialists in securing the continuous supply of high quality, digestible food required to fuel their large brains (Richard 1985). Richard (1965:121) proposes that "being a finicky eater with a big brain carries a host of implications not only for a primate's foraging behavior but also for its pattern of reproduction and social life".

With reference to the earlier discussion in this chapter addressing the social capabilities of nonhuman primates, it is also entirely possible that social pressures were an important factor in the evolution of the behavioral flexibility observed in these species. The very least that could be said is that the evolutionary significance of social cognition in nonhuman primates cannot be overlooked.

The Future

The subject of social cognition in primates seems to have sparked the interest of the psychological and primatological community. It seems, from all the scientific activity in this area, that the 1990s will be an exciting time for those of us interested in this area of research. I predict that there will be many more innovative experiments that will provide further proof of the social awareness of our nonhuman primate relatives.

The development of social cognition is clearly related to a number of contextual factors in the physical and social environments in which the infants are reared. My hope is that the methodology employed in this research project will be of use to other primatologists, particularly those working in the field. At the present time there are no detailed longitudinal studies of the day by day development of social or non-social cognition in free-ranging nonhuman primate species other than chimpanzees (Plooij 1982). The knowledge gained from this type of research would vastly enhance our ability to predict the effects of environmental agencies on the development of social skills. A beneficial byproduct of this knowledge would be an added awareness of the social needs of primate infants growing up in captivity. At the present time, when over fifty percent of nonhuman primate species are in some sort of jeopardy, either endangered or threatened, it would behoove us to concentrate our efforts on improving the lot of the animals over which we have some direct control.

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Appendix 1

Ethogram

States

These are ongoing, continuous behaviors which are recorded in terms of their occurrence and duration (Altmann 1974).They are mutually exclusive, and are arranged in order of their expected appearance over the observation period.

Nipple Contact - The infant maintains oral contact with the female's nipple.

Ventral Cling - The infant clings tightly to the ventral surface of a conspecific.

Ventral Cling, Head Loose - The infant clings tightly to the ventral surface of another, but the infant's head falls involuntarily away from the other's body.

Move on Body - The infant moves about on any part of another's body.

Wave Arms and Legs - The infant moves its arms and legs back and forth repeatedly, while clinging to another's body.

Open and Close Mouth - The infant opens and closes its mouth repeatedly while clinging to another's body.

Tongue Protrusion - The infant's tongue protrudes from its mouth while clinging to another's body.

Open and Close Hands - The infant opens and closes its hands repeatedly while supported on, or clinging to, another's body.

Suck Thumb Undirected - The infant inserts its thumb in its mouth and begins to suck when the thumb inadvertently touches the mouth.

Scratch Undirected - The infant's hand is flexed repeated beside a part of its body without making consistent contact with its body.

Muzzle (Receive) - A conspecific places its face in direct contact with the face or other body part of the infant

Groom - Hand (Receive) - The hair of the infant is parted and carefully searched through with the hands of a conspecific, who gives the activity its full attention.

Groom - Mouth (Receive) - The conspecific uses its mouth to part and comb through the hair of the infant.

Look Around and Cling - The infant moves its head back and forth alertly while supported on, or clinging to, another animal.

Head up - The infant holds it head up, away from the body of the animal to which it is clinging.

Look Around - The infant, while on its own, moves its head back and forth alertly.

Ventral Cling Loose - The infant clings loosely to the ventral surface of another animal, so that there is no direct ventral/ventral contact between the two animals.

Suck Thumb Directed - The thumb is sucked after it is inserted directly into the infant's mouth.

Scratch Directed - The back and forth movement of the infant's hand makes repeated and consistent contact with its body parts.

Clutch (Undirected) - The infant gropes for an object or portion of the substrate, eventually making contact with the desired goal.

Clutch Self (Undirected) - The animal gropes for a body-part, eventually making contact with desired goal.

Social Clutch (Undirected)- The infant gropes for a conspecific, eventually making contact with the other animal's body.

Oral Investigation - The infant licks or mouths an object or the substrate.

Social Oral Investigation - The infant licks or mouths a conspecific.

Lap - The infant sits between another animal's legs.

Crawl - The infant moves around on environmental surfaces on all four limbs.

Circle mother - The infant moves around and around the mother on all four limbs. .

Groom- Hand (Direct) - The infant grooms the other animal with its hands.

.**Groom-Mouth** (direct). The infant grooms the other animal with its mouth.

Muzzle (Direct) - The infant muzzles another animal.

Mutual Groom - The infant and the conspecific groom each other at the same time.

Self Clutch (Directed) - The infant clutches a part of its body without groping.

.**Clutch Object** (Directed) - The infant clutches an object or part of the substrate in a coordinated manner, without groping.

Social Clutch (Directed) - The infant clutches another animal in a coordinated manner, without groping.

Other Carry - The infant is grasped around the body and carried away by a conspecific.

Chew Object - The infant closes its mouth on objects or parts of the substrate and moves its jaws rhythmically.

Self Chew - The infant closes its mouth around a body part and moves its jaws rhythmically

Social Chew - The infant closes its mouth on a conspecific and moves its jaws rhythmically.

Dorsal Cling - The infant clings to, or rides on, the back of the mother or another conspecific.

Rejected from Body- The infant is rejected by the mother or another conspecific who tries to dislodge the infant from its body by moving around vigorously and pulling on it.

Social Watch - The infant looks intently at another individual from a close range.

Social Play - The infant repeatedly contacts, pushes, pulls, and otherwise vigorously interacts with a conspecific. This is often accompanied by a play face (see #111)

Solitary Play - The infant fiddles with an object repeatedly (drops, picks up, rolls, chews, etc.). This is often accompanied by a play face.

Tactile Investigation of the Environment - The infant feels or rubs it hand(s) repeatedly on an environmental surface.

Stand - The infant supports itself in an upright position on both legs, either unaided or by hanging on to a portion of the substrate or a conspecific.

Eat Solid Food - The infant places a food item in its mouth and chews until it disappears.

Hang/Swing - The infant suspends itself from a portion of the substrate by its hands, feet, or tail, remaining stationary or swinging back and forth.

Locomote - The infant moves across the substrate in a quadrupedal or bipedal manner. This includes walking and running.

Simple Climb - The infant moves directly up or down a portion of the substrate in an uncomplicated manner, using both hands and feet.

Self Groom (Mouth) - The infant grooms itself using its mouth and teeth as a comb.

Rub Hands Together - The infant puts its hands together and moves them back and forth repeatedly.

Complex Climb - The infant coordinates a number a motor actions sequentially, in order to move up and down a portion of the substrate; e.g., Hang, swing, move hand over foot or foot over hand, head first or feet first.

Rub and Chew - The infant moves a food item back and forth in its hands or on the substrate, then puts it in its mouth and chews. This behavior pattern is executed repeatedly.

Tactile Search for Dropped Item - The infant drops an item involuntarily and begins to search for it by feeling the environmental surface on which it dropped.

Simple Food Processing - The infant repeatedly rubs any food item on an environmental surface before eating.

Social Advance/Retreat Pattern - The infant repeatedly advances and retreats in response to a conspecific who is doing the same thing.

Close visual examination - The infant visually examines an object or food item from every angle.

Manipulation - An item or part of the environment is scratched, licked, turned over, rubbed and otherwise worked at by the individual. This activity appears to be directed at altering the state of the object being manipulated; e.g., twisting a twig off a branch.

Alternate Manipulation and Release - An item is alternately picked up, manipulated, and let go.

Urine Rub - Urine is dribbled onto the palm of the hands, then rubbed vigorously in the soles of the feet.

Locomotor Carry - The infant holds an object in one hand or foot, while moving across the substrate.

Locomotor Play - The infant displays a number of locomotor and postural actions in rapid succession. The actions are random, forming no particular purpose other than the pleasure derived from physical activity. This can be solitary play or play with a conspecific, in which case it involves alternate chasing and fleeing.

Complex Food Processing - The infant use specific actions to render particular food items easier to eat; e.g., banging a nut, rubbing a piece of fruit.

Wrestle/Rough and Tumble Play - The infant grapples vigorously with a conspecific with arms,legs, and mouth (Oppenheimer 1973). This activity is often accompanied by a play face.

Drink - The infant takes water from the environment directly into its mouth.

Mount (Receives) - the other animal stands behind the infant straddling it with its legs and "executes pelvic thrusting movements" (Oppenheimer 1973:263)

Mount (Directed) - The infant executes pelvic thrusting movements while clutching the back of another animal.

Chase (Receive) - Vigorous pursuit of the infant by a conspecific (Fedigan 1974).

Chase (Directed) - The infant vigorously pursues another animal.

Follow (Receive) - A conspecific moves steadily behind and in the path of the infant.

Follow (Direct) - The infant moves steadily behind and in the path of another animal.

Self Groom (Hand)- The infant grooms itself with its hands or mouth (see description of groom).

Wring Hands- The infants clasps is hands together in front of its chest and repeatedly moves them up and down (Oppenheimer 1973).

Grind Teeth - The infant "grinds premolar and molar teeth together producing an audible sound" (Oppenheimer 1973:263).

Display - The infant stands on all four limbs, facing the object of the display, threatening and rapidly raising and lowering its head and chest (Oppenheimer 1973).

Retrieve - The infant recovers an object that it has previously hidden or discarded.

Play with Water or Other Medium - The infant repeatedly slaps, jumps into, kicks, and otherwise interacts upon any environmental medium such as water or leaf litter.

Visual Search - The infant visually explores, probes, and rummages through the environment for specific items.

Experiments with Displacements - The infant uses trial and error actions with an object and field of force such as gravity.

Trial and Error Social Manipulation - The infant tries a number of actions to promote a desired effect on a conspecific.

Games - The infant repeatedly executes a series of locomotor actions in a particular pattern.

Selective Social Manipulation - The infant seeks out a specific animal for a particular interaction,

Rapid and Direct Choice of a Food Item - The infant moves rapidly and directly to a choice food item without trial and error manipulation of the food source.

Direct Choice of a Motor Action - The infant rapidly and directly moves in an appropriate manner to achieve an environmental goal; e.g., circumvent a barrier.

Deduction of Food Location - The infant moves directly and quickly to a remembered source of food. It is not guided by a visual perception of a conspecific or others.

Problem-Solving -When confronted with a novel situation, requiring the solution of a problem to achieve a goal, the infant is able to act in such a way as to achieve that goal.

Inactive - The infant is sitting, lying down, or sleeping. No activity is being performed (Fedigan 1984).

Events

These are single or transitory actions which may be repeated consecutively, and may be coincident with behavioral states.

Change of position - The infant moves on the mother's body, from side to side, dorsal to ventral surface, or vice versa.

Flex Hand or Foot - The infant stretches fingers or toes while clinging to the mother's body.

Startle Reaction - The infant jerks involuntarily as a reaction to a sudden noise or behavior.

Yawn - The infant's mouth is opened widely in a circular configuration.

Watch Dropped Item Fall - The infant attends visually to an item which has been dropped by itself or another individual.

Approach (Receive) - A direct advance of a conspecific towards the infant. Almost always preliminary to a social interaction (Fedigan 1974).

Approach (Direct) - The infant moves purposefully towards a conspecific.

Leave (Receive) - A conspecific moves away from the infant, after having been in close proximity to it.

Leave (Direct) - The infant moves away from the close proximity of another animal.

Drop Item Involuntarily - An item falls from the infant's hand or foot, with no obvious intent on the part of the infant,

Voluntary Drop - The infant drops an item, keeping visual contact with it from the time it leaves the infant's grasp until it touches a surface.

Pick Up Dropped Item - The infant moves to retrieve an item immediately after it has been dropped.

Restrain by Mother - The mother holds the infant by its tail or an appendage, thereby preventing it from leaving her.

Play Face Social - The infant opens its mouth and retracts its lips over its upper and lower teeth. Displayed in conjunction with an interaction with an other animal (Gouzoules 1980).

Play Face Non-Social - The infant opens mouth and retracts its lips over its upper and lower teeth. Displayed in conjunction with solitary play activities.

Pick Up Food - The infant grasps food from an environmental surface.

Object Grab - The infant reaches quickly and unsuccessfully for an object held by another animal.

Social Grab (Received) - A conspecific reaches out and clutches the infant.

Social Grab (Directed) - The infant reaches out and clutches another animal

Threat (Receive) - Facial expression directed towards the infant involving one or more of the following: hard stare, brow raised, ears back, mouth dropped open, vocalization (Fedigan 1984).

Threat (Direct) - The infant directs a threat to a conspecific.

Double Threat (Direct) - The infant places its head to the side or directly above that of a conspecific and delivers a threat simultaneously with the other animal.

Aggressive Action (Received). The infant is hit, pushed, or bitten by another animal (often accompanied by a threat face).

Aggressive Action (Directed). - The infant pushes, hits, or bites another animal (often accompanied by a threat face).

Seek Nipple - The infant attempts to fasten its mouth on the nipple of another female, usually its mother (Fedigan 1974).

Hop - The infant jumps up and down on the spot with its feet together.

Jump - The infant propels itself through space from one environmental surface to another.

Initiate Play - The infant attempts to draw another animal into a playful situation by touching, pushing, and otherwise making contact with the conspecific. This action is often accompanied by a play face.

Present for Groom - The infant lies on its back or ventrum, in close proximity to another animal, making itself accessible for grooming.

Imitate - The infant duplicates an activity being carried out by a conspecific.

Nipple Withdrawal (Received)- Removal of the nipple from the infant's mouth. This is accomplished by either pushing the infant's head away or by raising the arms, putting the nipple out of reach (Gouzoules 1980).

Steal - The infant quickly takes an object away from another animal.

Steal From - A conspecific forcibly takes an object away from the infant.

Hand to Foot or Hand to Hand transfer - The infant moves an object from one hand to the other or from a hand to a foot or vice versa (Parker 1977).

Planned activity - The behavioral unit immediately preceding this is executed for a specific purpose; e.g., to reach a food item.

Deposit - The infant places a food item or other object in a hole or aperture.

Retrieve Item - The infant removes a food item or other object from a place where it had previously been deposited.

Probe - The infant inserts its finger or hand in a hole or aperture or hollow end of an environmental object.

Fear Grimace - A visual signal in which the lips are retracted from the teeth, with the teeth clenched (Fedigan 1974).

Retreat - The infant moves away from a conspecific while facing it, by moving slowly backwards.

Appendix 2

The Weeks of Life Critical Behaviors were First Observed

Stage 1

Series Critical Behavior	Cebus	Patas	Lemur	Sq.M.
Sensorimotor Intelligence				
Nip.Cont.	B	B	B	B
Vent. Cling	B	B	B	B
Move on Mo.	2	B	B	B
Random Mov.	5	2	- (1)	B
Suck T. Undir.	-	2	-	-
Scratch Undir	-	2	-	B
	0-5	0-2	0-2	0-1
Object-Concept				
Nip.Cont.	B	B	B	B
Vent.Cling	B	B	B	B
Suck T.Undir.	-	2	2	-
Scratch Undir.	-	2	-	1
	0	0-2	0-2	0-1
No Observable Reaction to an Environmental Object				
Spatial				
Nip.Cont.	B	B	B	B
Vent.Cling	B	B	B	B
Move on Mo.	B	B	B	B
Change Posit.	B	B	B	B
Locomotor				
Move on Mother	2	B	B	B
Change Posit.	B	B	B	B
	0-2			
Social				
Grmed by Others	B	B	B	B
Muz by Others	B	B	B	B
Nip. Contact(Mo)	B	B	B	B
Vent, Cling (Mo)	B	B	B	B
Move on Mo.	2	B	B	B
Dorsal Cling(Mo) ** No Concept of others - only mother				

B - Present from Birth
**-Species-specific for Squirrel monkeys

Lemur () from Gould 1989.

Stage 2

Series Critical Behaviors	Cebus	Patas	Lemur	Sq.M.
Sensorimotor Intelligence				
Suck Th. Dir.	7	4	-	3
Scratch Dir.	6	5	5	3
Look Around	5	2	- (1)	3
Loose V.Cling	5	-	-	3
Feel Env.	7	3	-	3
Feel Body	6	2	-	-
	5-7	2-5	2-5	3+
Object Concept				
Feel Env.	7	3	-	3
Lick Surface	7	3	4 (3)	-
Chew Surface	7	3	6 (3)	4
Chew Body Part	8	2	4	4
Feel Body Part	6	2	-	4
	7-8	2-5	4-6 (3)	3-4
Spatial				
Loose V.Cling	5	-	- (1)	3
Look Around	5	2	- (1)	2
Feel Env.	7	3	- (3)	3
Lap Sit Mo.	9	3	- (2)	-
Sit Beside Mo.	8	2	- (2)	6
	5-12	2-3	(1-3)	2-6
Locomotor				
Crawl on Env.	7	2	- (2)	5
Crawl on Other	10	2	4	-
Circle Mo.	9	-	-	6
	7-9	2+	2-4	5-6
Social				
Feel Cagemate	7	-	7	3
Lap Other	-	2	6	-
Chew Other	9	3	-	7
Lick Other	8	3	-	4
	7-9	2-3	4-7	3-7

Lemur () from Gould 1989

Stage 3

Series Critical Behavior	Cebus	Patas	Lemur	Sq.M.
Sensorimotor Intelligence				
Clutch Env.	8	3	7 (5)	4
Eat Solid Food	10	3	4 (6)	4
*Self Groom (Mouth)	-	-	5 (4)	-
Pick up & Rel.	15	-	-	10
Play Face N.Soc.	8	-	-	-
Pick up Food	11	3	3 (3)	4
	8-15	3+	3-6 (3-6)	4-10
*Behavior specific to lemurs				
Object-Concept				
Clutch Env.	8	3	7 (5)	4
Solitary Play	8	4	10	7
Rub Surface	9	3	5	5
Pick up and Rel.	15	-	-	10
Pick up Food	11	3	3 (3)	4
Pick Up Drop.Item	13	7	7	11
	8-15	3-7	3-10	4-11
Spatial				
Dorsal Cling	9	5	2 (2)	(B)
Stand	10	4	5	5
Locomote	13	4	4	8
Climb	13	4	4	7
Away From Mo < 1M.	14	4	4 (4)	7
	9-14	4-5	(2-4)	5-8
Locomotor				
Hang	17	-	5(4)	7
Locomote	13	4	4	8
Climb	13	4	4	7
Hop	12	4	4	7
	12-17	4+	4+	7-9
Social				
Nip.Contact Other	10	-	8	-
Crawl on Other	-	-	4	-
Vent. Cling Other	-	3	4	-
Muzzle	8	-	-	3
Social Watch Mo.	-	-	-	6
Social Play Mo.	7	4	4 (6)	7
Social Play Others	8	4	4	10
Dorsal Cling Oth	12	6	4 (6)	6
Play Face Social	7	4	-	9
Social Clutch	8	7	5	3

Social Series continued

Series	Critical Behavior	Cebus	Patas	Lemur	Sq.M.
	Dir. Aggression	9	4	5	7
	Grab Object	9	3	10	6
	Threat	8	6	-	-
	Imitate	8	-	-	
		7-9	3-7	4-10(3-6)	3-10

* Behavior specific to lemurs

Lemur () from Gould 1989

Stage 4

Series	Critical Behavior	Cebus	Patas	Lemur	Sq.M
Sensorimotor Intelligence					
	Rub and Eat	18	-	-	-
	Simple Proces	18	7	-	11
	Close Visual Exam	18	-	6	12
		18+	7+	6+	11-12
Object-Concept					
	Rub and Eat	18	-	-	-
	Simple Proc.	18	7	-	11
	Close Visual Exam.	18	-	6	12
	Tactile Search	20	-	-	-
	Manipulation	18	7	7	8
	Self-Groom	23	7	-	18
	Hand/Hand	18	-	-	16
	* Urine Rub (Specific to Sq. Monkey)				10
		18-20	7+	6-7	8-16
Spatial					
	Complex Climb	18	6	5	7
	Loc. Play	19	-	5	10
	Jump	21	6	5	7
	Reverse	18	5	5	7
		18-21	5-6	5	7-10
Locomotor					
	Complex Climb	18	6	5	-
	Loc. Carry	20	7	14	11
	Loc. Play	19	-	5	10
	Jump	21	6	5	7
		18-21	6-7	5-14	7-11
Social					
	Groom Mo.(Hands)	18	7	N/A	-
	Visual Exam.Oth.	27	-	6	10
	Loc.Play Soc	25	-	5	16
	R.& T. Play	21	-	6	12
	Follow	18	4	4	9
	Seek Nipple Oth.	-	-	-	9
	Fear Grimace	31	-	-	-
	Initiate Play	21	-	-	10
		18-31	4-7	4-6	9-16

Stage 5

Series Critical Behavior	Cebus	Patas	Lemur	Sq.M
Sensorimotor Intelligence				
Complex Food Pr	24	-	-	15
Visual Search	20	-	-	-
	20-24	-	-	15+
Object Concept				
Displ.Experiments	32	-	-	-
Complex Food Pr.	24	-	-	15
Visual Search	20	-	-	-
Play with Medium	32	-	-	-
Insert Item	26	-	-	-
Retrieve Item	27	-	-	-
Hand in Aperture	29	-	-	-
	20-32	-	-	15+
Spatial				
Locomotor Game	35	-	-	-
Insert Item	27	-	-	-
Hand in Aperture	29	-	-	-
	26-35			
Locomotor				
Locomotor Games	35	-	-	-
	35+			
Social				
Selective Social	26	-	-	-
Display	34	-	-	-
Mount	26	-	-	14
Fight	-	-	13(12)	14
Pres.for Groom	22	-	14	-
**Double Threat	33	N/A	N/A	N/A
	22 +	-	13-14	14+

**Behavior specific to cebus monkeys

Lemur () from Gould 1989